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A comparison of field and growth chamber productivity of three poplar clones

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INTRODUCTION

Currently many parts of the world are experiencing shortages of wood fiber. Demands for industrial timber products in the U. S. rose 70% during the past three decades and substantial further increases are projected for the next 30 years. Potential demands are expected to increase from 13 billion cubic feet in 1970 to 23 billion cubic feet by the year 2000 (USDA Forest Research Report, 1974). Under current levels of forest management, only modest increases in timber supply will be available in future decades; this will be inadequate to meet projected demands (Josephson, 1973). Therefore, present shortages, coupled with projected increasing demand for wood fiber products, have caused researchers to examine new concepts for increasing the yields of fiber per acre. Concomitant with the shortage of fiber is the steadily shrinking land base available on which to meet the needed increases in productivity. Recent public interests in outdoor recreation activities, for example, have precipitated numerous resource use conflicts.

One new concept to meet the increased need for fiber currently under investigation at Iowa State University, in cooperation with the North Central Forest Experiment Station of the United States Forest Service, involves growing trees in an agronomic mode, characterized by high plant densities, short rotations, and intensive silvicultural treatments, such as maintaining high levels of nutrients and moisture in the field (McAlpine et al., 1966). Growing trees in this "woody plant agri-system" could help to meet increased fiber needs, in conjunction with other partial solutions such as increased harvesting of existing timber lands, recycling, or use of agricultural by-products and annual crops for paper pulp. In practice,

trees would be grown for less than ten years and then mechanically harvested. Only trees that have rapid juvenile growth and coppice regeneration ability would be considered for use in this system. In the North Central region, particular attention is being given to hybrid poplars as a source of wood fiber. Besides meeting the previously mentioned criteria, use of these rapidly growing trees would enable large amounts of fiber to be produced per acre on smaller, more concentrated areas of land and thereby make it possible to divert the residual land to uses other than fiber production. Thus, conflicts over the use of public and private lands might be minimized.

To provide information needed for the practical use of hybrid poplars in intensive silviculture systems, the genetic, physiological, and field growth characteristics of several poplar clones have already been studied. Particular effort has been made to first define the environmental factors most important in determining yield and to define their relationships to each other and to yield and second to devise methods to select rapidly given clones to best fit these previously defined growing environments, where nitrogen, minerals, and water conditions would be kept in near-optimum supply. Work at Iowa State University has been done to specify selection criteria based on growth and nitrogen relations (Dykstra, 1972), response to temperature and soil water (Domingo and Gordon, 1974), leaf arrangement and display (Max, 1975), peroxidase activity (Wray, 1974) and rates of photosynthesis and light and dark respiration (Domingo and Gordon, 1974; Gjerstad, 1975). Current work is concerned with examining response of clones to various light intensities (important in mixed plantations), as

well as with studying environmental effects on photosynthate distribution within both individual trees and the total stand.

In this study, I have attempted to define the relationships between growth room and field productivity for three hybrid poplars when only the photoperiodic conditions in the field were roughly approximated in the growth chamber. The use of controlled environments is particularly valuable in examining the effects of individual environmental components on the control of growth processes in a way not rapidly possible in the field. For example, insight into the relationships between regulation of dormancy and environmental parameters can be obtained over a wide range of conditions not found frequently in the field through the use of controlled environments. Furthermore, in defining these relationships, it might be possible to more effectively match individual clones with optimum environments in the field, i.e., to match growth periodicity with the growing season.

If controlled environment growth studies could be used to predict field performance of clonal material, great savings would result. This is particularly true in the screening of the thousands of possible Populus clones that could be useful in woody plant agri-systems. Because of the generally favorable field growing conditions in intensively cultured stands, it was felt that controlled environment facilities should have a better chance of producing growth responses similar to field responses than with conventional field systems using long rotations and low cultural levels.

Although differences between the controlled environment and the field were recognized, it was felt that by choosing the proper variables and controlled environments, field growth potential might be estimated without

close simulation of field growth conditions. The ultimate objective of this study was to develop a technique of rapid selection of those clones that might be expected to do best in given field locations by means of a preliminary analysis of selected variables under growth room conditions.

It is recognized that controlled environments are not singularly the final answer to selection; results from controlled environments will be compared with field trails at a number of locations and the combined data will be fitted into models currently being designed by other workers to enable yield predictions over a wide range of conditions.

This study will provide basic data about the relationship of growth in controlled environment to growth in the field. An insight into the potential for using controlled environments as rapid selection tools will be provided and this information will be helpful to people doing pilot scale work in woody plant agri-systems in the North Central Region.

LITERATURE REVIEW

Existence of Photoperiodic Ecotypes

The response in growth and development exhibited by plants in relation to the length of the daily light period (the photoperiod) is called photoperiodism (Pauley and Perry, 1954; Garner and Allard, 1923). The first recognition of the influence of day-length of reproductive development in plants was made by Garner and Allard (1920) in tobacco. Later Garner and Allard (1923) observed that the relative duration of days and nights regulated the growth of several woody species in summer and fall. Plants of Liriodendron tulipifera L. transferred to a greenhouse in September and given supplementary light resumed growth for 18 continuous months; plants not given the additional light remained dormant throughout the winter. The existance of a capacity for photoperiodic response in woody species was thus first demonstrated.

Today the vegetative growth of many woody plants is known to be controlled by the relative length of the daily light and dark periods. In woody plants, as well as in herbaceous plants, the length of the unbroken dark period seems to be a critical factor in the photoperiodic phenomenon (Vaartaja, 1957). In general, long days prolong the growing period and short days inhibit growth and induce dormancy (Bogdanov, 1931; Downs and Piringer, 1958; Moshkov (cited in Gevorkiantz and Roe), 1935).

The details of the response to photoperiod vary markedly with species, however (Downs and Borthwick, 1956). In addition, the photoperiodic response of a given species depends upon the geographic origin of the seeds

or other properties of the material (Pauley and Perry, 1954; Downs and Piringer et al., 1958).

The photoperiodic ecotype is a population that has, during evolution, adapted itself to its seasonally changing environment through a photoperiodic stimulus in a way different from the adaption in other populations within the species. The photoperiodic ecotype likely has evolved and functions mainly as an indirect mechanism for adapting the plant to various seasonal changes and to factors other than the photoperiod itself (Vaartaja, 1959). In other words, photoperiodic ecotypes in nature function to regulate a safe timing for the alternation of the active growth stage, which is susceptible to cold and drought and the dormant stage, which is hardy (Vaartaja, 1960b, 1961).

Because the day length of the warm season in general is long in the high (northern) latitudes and short in the low (southern) latitudes, it is to be expected that northern and southern trees have evolved with different responses to photoperiod. If differential evolution has taken place within a species, the northern and southern populations may be considered different ecotypes (Vaartaja, 1960a).

Evidence to support the theory of photoperiodic ecotypes in Populus tremula L. was first shown by Sylven (1940), who reported that seedlings of this species, obtained by crossing parental trees from different parts of Sweden, reacted differently to the natural and 12-hour photoperiod, depending on the photoclimate of the origin of the parents. Strains of Populus tremula L. from varying locations in Sweden differing by two to three degrees in latitude showed genetic differences with respect to photoperiodic effects (Sylven, in Wareing, 1949a).

Vaartaja (1954) grew several woody species at two widely different latitudes and hence two different photoperiods. He found that the northern species grew best in the long days and the southern species grew best in the short days. Since the days at the northern latitudes are extremely long and those in the southern latitudes relatively short, Vaartaja explained the growth differences as a result of heritable adaptation by the tree. He concluded that within tree species there are photoperiodic ecotypes, which during evolution have adapted themselves to the photoclimate of their environment.

In further tests of seed source-photoperiodic treatment interactions, Vaartaja (1962) found that tests with northern (above 30-40 degrees latitude) tree species all showed this interaction and that it followed a certain pattern which could be explained as an adaptation mechanism. For example, a certain short day-length inhibited northern seedlings more than southern seedlings, thus giving evidence of photoperiodic ecotypes in northern tree species. Similarly, in northern ecotypes dormancy is induced by a longer day-length than in southern ecotypes (Vaartaja, 1959, 1961). This agreed with Downs and Borthwick (1956) who found evidence of photoperiodic ecotypes in first year loblolly and ponderosa pine. Further, Vaartaja (1960b) found that the responses to various photoperiodic treatments, ranging from an extremely short day to an extremely long day, were well correlated with the latitude of seed source, i.e., the farther north the origin, the more was the growth suppressed by extremely short days. These results were in agreement with those of Pauley (1957), Downs and Piringer (1958), Pauley and Perry (1954), and Wassink and Weirsma (1955), who found that the time of cessation of extension growth was inversely cor-

related with the latitude or day-length of the frost-free season of the native habitat. Vaartaja (1960a), using cottonwood (Populus deltoides) and quaking aspen (Populus tremuloides Mich. x) seeds from 30 degrees N and 45 degrees N latitude, also confirmed the finding.

The severity of winter and the length of the warm season, of course, are usually in close correlation with latitudes and hence photoperiod, except in mountainous regions (Vaartaja, 1959) and areas near large bodies of water. In these regions plants from high altitude, short growing season ecotypes (e.g., Rocky Mountains region) may terminate growth similarly to ecotypes from high latitude, long day plants (Pauley, 1952).

Similar ecotypic variation was reported within the North American species of Populus tacamahaca, Populus deltoides, and Populus trichocarpa (Pauley and Perry, 1954). Hybridization between ecotypes and artificial alternation of the photoperiod showed that the duration of terminal growth is controlled by the interaction of the genotype and the environment (Perry, 1953). Pauley (1952) reported that hybrids between parents from a northern and southern ecotype terminated growth at an intermediate time relative to the parental material, when all were grown under a uniform day-length.

Vaartaja (1959) cautioned that until the physiological processes that operate in the photoperiodic response and in the adaptation mechanism are known, the hypothesis of photoperiodic ecotypes must remain descriptive rather than causative.

Relocation of Plants from Native Origin

Many researchers have attempted to test the interaction of seed source and photoperiodic response by moving plants out of their native photoperiodic ecotype into latitudinally different areas. In theory, if plants are moved out of their natural range northward or southward and growth is found to be prolonged in long days and curtailed in short days, the conclusion may be made that the growth response is photoperiodically sensitive.

In general, it may be said that when plants are moved north of their natural habitat (hence longer days), the active period of growth is prolonged and movement of the plants south shortens the active period of growth (Pauley and Perry, 1954; Wareing, 1953). This was tested by Moshkov (1930), who found frost resistance to be one of the principle factors governing the northward range of woody plants; this depended to a considerable degree on the response to the length of day.

Sylven (1940) and Wareing (1949a) showed that within the species Populus tremula L., the races from northern Sweden differed in photoperiodic response from those of southern Sweden and that when northern strains were grown in the south, they showed reduced growth and stunting while southern strains grown in the north showed delayed dormancy and were damaged by autumn frosts.

Using various clones of Populus spp., Pauley (1952) and Pauley and Perry (1954) found that high latitude, long day clones, when moved southward into shorter days, ceased height growth abnormally early, resulting in dwarfed clones, even though otherwise favorable growing conditions existed for many months. Conversely, movement of clones northward into abnormally

long days resulted in plants with increased height growth but low resistance to frost damage (Pauley, 1957).

These results are in agreement with Kramer (1936) who found that dormancy was hastened by short days in all woody species examined except Quercus alba L. and that long days delayed dormancy in the majority of species, as compared with natural day-lengths.

Even in the case of Pinus spp. (e.g., P. sylvestris), where after the first year the number of nodes is predetermined by the number of initials laid down in the buds in the previous year, the extension of internodes is affected by photoperiod, being reduced under short day conditions (Wareing, 1950b). Extension of needle growth is also reduced under short day conditions (Wareing, 1949a).

Kramer (1943) further found that northern trees, when moved south of their natural origin, started second year growth sooner and also ceased growth earlier in July and August. Therefore, many northern species moved south used only one-half to one-third of the growing season. However, Jester and Kramer (1939) reported that the growing period of two species, Fraxinus americana and Quercus borealis, were not affected by long days.

In 1957 Vaartaja reported an experiment using ten tree species and two photoperiods with otherwise optimum conditions. In long days, all plants grew well; in short days, however, there was a varied response. Some species (larch, elm, fir) became dormant, some reduced growth (Betula, red pine), and some grew regardless of the reduced photoperiod (Caragana, Thuja, Acer negundo).

Vaartaja (1960a) tested several species for photoperiodic sensitivity by means of moving plants north and south of their native range. In the

northern test, the native northern trees produced less height growth than the transplanted southern species, evidently because the northern trees possessed a safety margin against abnormally cold weather and became dormant as a response to the day-length of a certain date when damaging cold normally does not occur. Significantly many of the southern trees failed to set bud in time for cold weather and were killed.

Nienstaedt and Olson (1961) and Pauley (1952) reported similar results. Transplanted southern ecotypes made as much as 600% more growth than their native northern relatives but continued to grow into fall when frost caused high mortality. Vaartaja (1959) related evidence from Finnish trials showing that trees moved south slowed growth but survived, while those moved north more than a few hundred miles suffered frost damage. This also agreed with statements by Gevorkiantz and Roe (1935). Vaartaja (1959) cautioned that foresters should not plant seeds or seedlings too far away from their point of origin for these reasons. Losses in wood production can be expected if plants from areas with short growing seasons are grown in areas with a longer growing season, due to increased frost susceptibility (Holst and Yeatman, 1961). Movement should be limited to a few hundred miles (Vaartaja, 1959). Langlet (1959) stated that the risk of a seed transfer from a mature stand to a site with a different temperature and day-length climate must be judged in relation to the variation of the species.

Marked genetic differences in growth and other characteristics are expressed when populations are grown at latitudes substantially different from that of their native habitat. For example, transfer of seedlings out of their natural range has been found to alter basic morphological charac-

teristics. These include duration of height growth (Downs and Borthwick, 1956), internode extension, leaf growth in conifers (Wareing, 1949a, 1950a,b), time of leaf abscission, duration of cambial activity (Wareing, 1956), branching length and display (Gevorkiantz and Roe, 1935; Olmstead, 1944; Nitsch, 1957a), leaf shape (Nitsch, 1957a) and root development and bud activity (Gevorkiantz and Roe, 1935). Olmsted (1944) grew 12 strains of oats from latitudes differing by 17° and found the development of the primary axis was highly correlated with latitude of origin. He suggested that correlations might be worked out relating the effect of different photoperiods on seedling behavior which would make it possible to make early selections for "earliness" and "lateness." These conclusions were also substantiated by Larsen (1947) who grew strains of grasses from a wide latitude of seed sources under varying photoperiods. Under the 13-hour photoperiod, none of the plants flowered, while under the 14-hour photoperiod southern strains elongated and flowered, with northern plants being inhibited; under the 15-hour photoperiod, both northern and southern plants grew and flowered. Thus, the existence of a critical photoperiod was established for these species.

In reference to photoperiodic control of leaf area, Olmsted (1951) reported greater leaf area in controlled long-day environments (20 hour) as opposed to a shorter (9 hour) photoperiod.

Fowler (1961) reported that height and amount of root growth were strongly controlled by the photoperiod, whereas stem diameter and oven dry weight were dependent upon both the photoperiod and the light intensity.

Moshkov (1930) reported that short day exposure of locust (Robinia pseudoacacia) gave scales instead of thorns, unnatural leaf color, and a

considerable increase in root weight. Nitsch (1957a) reported that long-day photoperiods given during the rooting period caused an increase in the extent of rooting as measured by the number and length of roots produced. Nitsch further pointed out that the photoperiodic regime to which stock plants had been exposed exerted a marked effect on the ability of cuttings to root. He found that cuttings of Salix undulata rooted 100% from stock plants given an 18-hour photoperiod while cuttings from those plants given a 9-hour photoperiod gave zero percent rooting (Nitsch, 1957a, 1961). Branch cuttings taken from stock plants exposed to 15-, 14-, 13-, and 12-hour photoperiods gave progressively fewer roots. As the days became shorter in the fall, rooting capacity of poplar branch cuttings decreased. Wareing (1950a), however, reported no differences in rooting of cuttings taken from Pinus sylvestris plants exposed to either a 10- or 15-hour photoperiod. Hellmers and Pharis (1968) experimented with several photoperiods on 24- and 48-hour cycles. The distribution of shoot to root weight was only slightly affected by either the photoperiods or the cycles.

Wassink and Wiersma (1955) reported that Pinus sylvestris from southern regions grew well in 12- or 24-hour days and that southern plants showed a positive correlation of size and extent of root system. Northern strains showed no correlation.

In Populus spp., short days cause the transformation of leaf primordia into scales (Nitsch, 1957b, 1961), while in the case of P. canadensis the elongation of the internodes separating already unfolded leaves may continue for a short time. Transfer of Weigela florida, Betula pubescens or Cornus from long days to short days resulted in growth stoppage within two weeks (Nitsch, 1961; Waxman, 1957).

The duration of cambial activity has also been shown to be related to the photoperiodic regime. Wareing (1951) reported that even though extension growth in Pinus sylvestris was completed in June, cambial activity continued until late October. With supplementary illumination, evidence of an active cambium could be found until late November. Cambial activity could be maintained in the greenhouse under short days supplemented with quite low light intensity illumination so that the effects were not due to photosynthetic differences (Wareing and Roberts, 1956). These differences were thought to be due to variations in auxin content in the plants (Wareing, 1949b; Wareing and Roberts, 1956). Digby and Wareing (1966) examined both ring porous and diffuse porous trees and established a positive correlation between amount of cambial activity and auxin. Giberellic acid was also found to be involved in the control of phloem differentiation. Priestly (1930) had earlier observed a correlation between the initiation of cambial activity and the resumption of growth of the buds in the spring and that activation proceeded basepitally.

Evidence has been presented that ecotypic differences also exist not only between different latitudes but within the same latitudes (Pauley, 1957). There is great diversity among local habitats with respect to the length of the growing season within any particular latitude. A positive correlation was found between the length of the growing season in the native habitat and the time of height growth cessation at the test site (Pauley, 1957). Such evidence of local ecotypic diversity in the growth cessation response lends strong support to the hypothesis that adaptation to the length of the growing season in a uniform day-length zone is affected by natural selection of those genotypes possessing the best photo-

periodic response commensurate with optimal growth and development in the growing season of the particular native habitat (Pauley, 1957). Results of Downs and Borthwick (1956) agreed with this interpretation. They found that variation between species in response to different photoperiods depended on the time at which growth stopped in nature. Species which stopped growth naturally in June or July were least sensitive to long days; plants which grew naturally until the frost were least sensitive to short day treatment. Nienstaedt and Olson (1961) reported that for any given regime of day and night lengths, seedlings from regions of long frost-free periods tended to form rest buds later than those from regions of short frost-free periods. Therefore, ecotypes native to long growing season habitats in any particular latitude should be avoided as seed sources for short season habitats at the same latitude because of this susceptibility to early autumn frosts.

The use of gene combinations closely adapted for full utilization of the growing season in a particular habitat, as a means of increasing net yields of fiber, is promising (Pauley and Perry, 1954). Presumably, selection operated on the genotype to give optimum duration of extension growth under the day-length conditions prevailing in any one region. If species are transferred to regions of different latitudes, however, the mean day-length conditions throughout the period of growth will be altered and will affect the duration of extension growth (Wareing, 1956). It is clear that photoperiodism has important implications for the breeding of forest trees for new types must show the same delicate adjustment to day-length as is found in natural ecotypes (Wareing, 1956).

Attempts have been made by various researchers to classify woody species based on the effectiveness of long days in bringing about continuous growth and of short days in causing complete cessation of growth. Chouard (1955) classified all Populus spp. in "Class A," where long days prevent the onset of dormancy and short days cause dormancy. Wareing (1949a) classified species according to the duration of the growing period in relation to the natural day-length. He recognized three main groups: species in which stem growth remains continuously active until September or October; species in which growth ceases in July or August; species in which growth ceases in May or June. Movement of species into unadapted areas would, of course, cause disruption of this scheme.

In considering the effect of day-length on growth, it should be recognized that this is only one aspect of the control of extension growth. Other factors must be considered, such as temperature, soil fertility and water relations and in many species the duration of extension growth is apparently also affected by certain endogenous processes (Wareing, 1956). The overall period of growth is determined by the interaction of endogenous and external functions (Wareing, 1956; Nienstaedt and Olson, 1961). Although Vaartaja (1959) said growth patterns and dormancy of trees were obviously affected by an endogenous rhythm, he also stated that the relationship between photoperiodic ecotypes and endogenously different growth patterns is unclear. He further stated that this endogenous growth pattern could either be modified or entirely obscured by the effects of photoperiodism in many cases. In red pine, the growth of the species follows an endogenously determined growth patterns, which cannot be fully overridden by photoperiodic treatments (Vaartaja, 1962). In many species from north-

ern latitudes (Alnus, Acer spp.), extension growth ceases in May or June before there has been any appreciable reduction in the natural day-length (Wareing, 1956; Kramer, 1943). Here day-length conditions are not limiting, so growth may be controlled endogenously, assuming water and nutrients are not growth limiting. Downs and Borthwick (1956) and Nienstaedt and Olson (1961) alluded to the phenomenon of endogenously controlled growth patterns when they stated that some species stop growing even on long days or in continuous light, indicating that in such cases some factor other than the photoperiod may be exercising control; that is, an inherent physiological mechanism that becomes effective as the season progresses.

In summary, it is not known exactly how the process of photoperiodic timing functions but it is believed to involve one or more oscillating timers dependent on endogenous rhythms (Hillman, 1969). The duration of extension growth also depends on the age of the tree, the position of the shoot and the cultural conditions (Klebs, 1914; Wareing, 1949b). Presumably in older trees competition exists within the tree for nutrients and this may bring about the cessation of growth (Wareing, 1956; Wareing and Saunders, 1971). Wareing further cautioned that because of factors such as this, conclusions regarding older trees cannot be arrived at by extrapolation from the photoperiodic behavior of seedlings. Little is known about the relationship between nutritional factors, for example, and the changes of growth activity in plants grown under different photoperiods. Abundant nitrogen fertilizer stimulates seedlings so that they will grow into the late fall (Wareing, 1969); thus, the normal response to short day photoperiods is apparently somewhat altered by the internal nutrient status of the plant. Fowler (1961) tested three levels of soil fertility and found

growth of white pine depended on the fertility and this dependence increased as other conditions (for example, the photoperiod) improved.

Photoperiod and Temperature Interactions

In nature, the photoperiodic response in trees is likely masked and modified by many factors, especially by temperature (Vaartaja, 1960a). Many tests of photoperiodic behavior in the field may be confounded in the summer and less growth difference may be apparent due to high (greater than 90° F) temperatures. Also, photoperiodic ecotypes react to temperature in different ways and thus lead to the postulation of temperature-photoperiodic ecotypes or "physiological ecotypes" (Downs and Piringer, 1958). The fact that the temperature has a strong modifying influence on the photoperiodic phenomenon is illustrated by Waxman (1957) who found that in "Class A" plants, the photoperiodic response was clear-cut when minimum night temperatures were 21° C. At a temperature of 10° C, however, only the longest (21- and 24-hour) photoperiods were able to produce optimum growth. Nitsch (1961) found that a temperature of 10° C prevented photoperiodic responses from occurring that would have occurred at higher temperature when Robina pseudoacacia was transferred from long days to short days at four temperature levels.

Much of the information about photoperiod-temperature interactions has come from provenance tests. A provenance test is a comparison of the morphological and physiological characteristics of a number of population samples of a tree species when they are grown under uniform conditions of soil and climate (Holst and Yeatman, 1961). These authors grew Pinus banksiana seed from sources at 44° north and 50° north latitude and correlated height

growth with two indices: (1) length of the growing season, given as the number of days per year that the mean daily temperature exceeded a base of 42° F and (2) the mean temperature for the months June, July and August. They found that height growth of the transplants was positively correlated with the length of the growing seasons and the mean temperature of the locality of origin. Thus, evidence was presented for both photoperiodic and thermoperiodic ecotypes. In another experiment using jack pine seedlings, height growth was positively correlated with latitude and the number of degree days over 50° F per year at the area of origin (Stoeckler and Rudolf, 1956). These results were also confirmed by Giertych and Farrar (1962), who measured height and dry weights of plants and correlated these with (1) the latitude or number of hours daylight on the longest day and (2) the number of growing degree-days per year. As both variables increased for the place of seed origin, the size of the seedlings increased. The marked response of the northern provenances to the photoperiodic treatments supports Vaartaja's contention (1959) that the more severe the climatic conditions are, the more essential is an adaption to a photoperiodic stimulus which prepares the plants for drought or cold; however, such an adaption also prevents the plant from making full use of the growing season in most years (Giertych and Farrar, 1961; Kramer, 1943). In a test of photoperiod, temperature and seed source interactions, Jensen and Gatherum (1965) observed that for Pinus sylvestris the genetically determined characteristics of the various seed sources were affected differently by temperature and photoperiod. They found that height growth increased with longer photoperiod from 12 to 20 hours, with greater response at 56° F versus 71° F. However, height growth at 12 hours was better at the 71°

temperature. Thus, in this case, photoperiod and temperature were interchangeable within certain limits. Jensen cautioned that the existence and magnitude of these interactions should be known when variants within species are grown outside their natural range.

Farmer (1963) tested the effect of light intensity and temperature on growth of Populus tremuloides. He found that at the lower (500 foot candles) light intensity, better growth occurred at a lower (70 degrees/ 66 degrees day-night) temperature than at the higher (76/71 degree) temperature. He surmised that reduced growth occurred in the higher temperatures due to increased rates of respiration. Kramer (1957) found that higher day temperature increased shoot growth; high night temperature reduced it. Kramer hypothesized that warmer nights induced internal physiological changes which lead to dormancy.

Another example of how temperature exerts an important modifying influence on the photoperiod is seen in the control of leaf abscission. Leaf abscission is affected by day-length conditions in certain deciduous species, the normal time of leaf fall being delayed when natural day-length conditions are extended with supplementary light or hastened by short day treatment (Matzke, 1936; Wareing, 1956). In natural conditions, the effect of photoperiod in controlling leaf abscission is confounded by lowered temperatures in the fall. Thus, some plants grown in a greenhouse dropped their leaves at the normal time under natural autumn day-length conditions but retained them throughout the winter under long days (Garner and Allard, 1923). Other seedlings have been found to retain their leaves for long periods of time under short days when maintained under warm conditions (Wareing, 1954). Nitsch (1957a) found that if the night temperature was

lowered to 10-15° C, while days were kept short (9-12 hours), dogwood leaves turned a brilliant red color before senescing.

Leaf shape has been found to change with different photoperiod-temperature combinations. High temperatures and long days gave undulating leaves in peach, while short days and low temperatures led to long, narrow leaves (Nitsch, 1957a). Increased mesophyll growth was thought to lead to wavy leaves in long days, while vein growth was accelerated in short days leading to narrow leaves.

Photoperiod, Temperature and the Breaking of Dormancy

Dormancy is typically a phase which shows specific adaptation to adverse environmental conditions (Wareing, 1969). Much confusion arises in interpreting results of photoperiod and temperature interactions in relation to the breaking of dormancy in woody plants, principally because many researchers fail to distinguish between different forms of dormancy. In considering this problem, it is important to make a distinction (a) between buds which are in a state of summer dormancy and those in winter dormancy and (b) between chilled and unchilled winter resting buds (Wareing, 1956).

Specific forms of dormancy further can be considered within these broad categories. For purposes of subsequent discussion, these dormancy states will be considered (Wareing, 1969): quiescence, or imposed dormancy, is the arrest of active growth due to external environmental conditions (such as unfavorable temperature or water), whereas innate dormancy, or rest, is when growth is arrested even though environmental conditions appear to be favorable. For example, many temperate tree species form resting buds in August. However, only visible elongation ceases; cambial

growth may continue (Samish, 1954). Further dormancy classifications are predormancy (early rest) when the organ can be induced to resume growth and postdormancy (after rest) when it becomes progressively easier for the organ to resume growth (Samish, 1954; Wareing, 1969). Buds formed under long days are first in the predormancy state, because they will expand prematurely under appropriate conditions (defoliation, for example). Buds in a state of summer dormancy are much more easily induced to break by long day treatment than buds in the winter dormancy condition, as shown by Wareing (1956) for Pinus sylvestris. Once this species entered a state of winter dormancy, it would not respond to long day treatment at all times, regardless of the state of dormancy.

Van der Veen (1951) suggested that the state of dormancy increased during the period following the stoppage of growth, thus perhaps explaining why some researchers have reported that dormancy could be broken with long days and some have reported that it could not. Likewise Vegis (1964) suggested that as predormancy progresses, the range of external conditions under which plants are able to grow becomes more and more narrow. For plants coming out of dormancy in the spring, the opposite conditions exist. The transformation from predormancy to true dormancy occurs during the middle phase of the rest period when depression of growth activity is the strongest. It would appear, therefore, that there are marked differences between species in their capacity to respond to continuous illumination by breaking dormancy (Wareing, 1956). Short days generally promote dormancy. When fully dormant, buds of many woody species require a period of chilling before growth can be resumed (Vegis, 1964). Samish (1954) reported the range most effective was 1 to 10° C for from 260 to 1,000 hours.

That there are differences between chilled and unchilled buds were shown by VanderVeen (1951), who was able to induce unchilled seedlings of Populus robusta to break dormancy by exposure to continuous illumination but only after a delay of several months. However, chilled buds in Populus spp. readily break dormancy under all day-length conditions and even in continuous darkness if proper temperatures are given (Pauley and Perry, 1954; Wareing, 1956; McMillian, 1957).

Wareing (1951) reported that dormancy could be broken in Pinus sylvestris plants that had been prevented from exposure to chilling temperatures by means of 18-20 hour photoperiod; however, breaking was much easier if the plants had first been subjected to chilling temperatures. Similarly, Nienstaedt and Olson (1957) reported that long photoperiods could partially compensate for lack of chilling. Plants brought inside in October after bud set responded to long photoperiods and broke bud even when not artificially chilled; however, the time to break bud in unchilled plants was two to three times longer than for those fully chilled. Klebs (1914) reported that under conditions of continuous artificial illumination, beech (Fagus sylvatica L.) could be induced to break dormancy in September following bud set and under such conditions could be kept growing continuously throughout the winter. Wareing (1953) stated that in some species (Betula, Fagus) bud dormancy could be overcome by transferring the seedlings from short days to long days. Therefore, the buds themselves were capable of responding to the long photoperiods because even leafless seedlings resumed growth. Buds of Fagus showed no change in photoperiodic requirements for breaking dormancy even after prolonged periods of chilling at 0-5° C (Roberts and Main, 1965). As beech buds apparently had no chilling

requirement, Wareing suggested that the time of bud break in some regions might be controlled by seasonal changes in the photoperiod. Downs and Borthwick (1956) said that in dogwood exposure to long photoperiods could replace the need for a cold period; in birch it was found that the terminal bud required a cold period to overcome rest but that the axillary buds did not. Wang and Perry (1958) felt that the photoperiod exercised a controlling influence over the continuation of shoot elongation and the onset of dormancy. There was no indication, however, that the time of growth initiation was influenced by photoperiod except possibly in unchilled plants. Salisbury and Ross (1969) reported that it was possible in many woody species, if not all, to demonstrate a clear-cut control of the dormancy phenomenon by the photoperiod, especially if temperatures remained high.

Farmer (1968) found that Liquidambar styraciflua seedlings rapidly resumed growth when placed under greenhouse conditions if they had previously been chilled at 3° C from 12-1,600 hours. Again, long photoperiods were effective substitutes for chilling. Farmer further reported that the chilling requirements of various seedlings were associated with the latitude of seed source; low latitude (31°) plants had a lower chilling requirement for bud break than those from a higher (36°) latitude. In all cases, the growth rate under long photoperiods varied directly with the length of the previous chilling period. McMillian (1957) suggested that the initiating stimulus for bud break is genetically controlled and that it is possible that different periods of cold are required for bud opening by different populations of one species. He took twigs from five woodland communities in the winter and brought them into a greenhouse. Each species

(Acer, Ulmus, Populus, Fraxinus, Quercus) opened buds under greenhouse conditions in a sequence repeated at later dates at the community sites.

Gustafson (1938) found that plants of Pinus resinosa which had been allowed to remain out of doors during the winter broke dormancy in the normal way under natural day-length conditions in the spring but that plants which had been protected from low temperatures during the winter showed no new shoot growth under natural day-length but did so if the photoperiod was increased to 16 hours. Thus it was possible to achieve the breaking of dormancy by exposure either to low temperatures or long days. Several investigators have shown that long days alone will break dormancy of trees of certain species but these differ widely in the relative duration of the photoperiod treatment required to induce the resumption of growth (Downs and Borthwick, 1956).

Pauley and Perry (1954) stated that although light exerts a profound influence on growth activity during a large portion of the growing season in Populus spp., neither light or its periodicity appears to be directly concerned in the break of dormancy. Pauley (1957) modified this statement to say that seedlings must first be properly chilled for this to be true in some woody plants (poplars). McMillian (1957) and Lavender and Hermann (1970) also stated that buds whose chilling requirements were fully satisfied initiated growth in response to favorable temperatures rather than long photoperiods. The differences in flushing of clones was said to be a response to the prevailing temperatures, acting quite independently of the light environment. These authors concluded that photoperiod is ineffective in the breaking of dormancy in the spring of Populus. Later a "critical photoperiod" is reached which coincides with favorable temperatures to

allow bud break. Stated another way, by the date when temperatures have risen sufficiently to permit growth, the length of the natural day is no longer a limiting factor (Kramer, 1936). Kramer further stated that in the majority of species, the seasonal rise in temperature is the determining factor in the time of bud break in the spring.

Olmsted (1951) found no correlation between photoperiod and either entrance into rest or the end of rest in the spring. Olmsted felt that the fact that the date of spring growth from a leafless branch was not influenced by day-length was expected, since no leaves were present to receive a light stimulus. However, plants also did not react to long days when entering rest, indicating to Olmsted that photoperiod was not a factor universally involved in rest. Terminal growth was stopped, with winter buds formed in photoperiods ranging from 8-20 hours and while natural photoperiods were increasing or decreasing, indicating bud rest under natural conditions was not decisively related to photoperiod. In sugar maple, the duration of terminal growth was similar for first flushes regardless of the photoperiod.

Phillips (1941) stated that temperature did not appear to be the limiting factor in growth when kept within the ranges necessary for plant growth activity. Phillips based this statement on the fact that some woody plants, when brought into a greenhouse environment and kept at favorable temperatures during the winter, frequently exhibited dormancy. It is not known if chilling requirements had been met in these plants. Further, it is suggested by several workers that plants have indirectly adapted themselves to temperature conditions by means of the photoperiod. In Phillips' work, the plants were exposed to the winter photoperiodic conditions and

not to artificially increased day-lengths. Hence, the plants were exposed to a day-length below the critical photoperiod. At day-lengths below this critical level, vegetative growth is arrested (Pauley and Perry, 1954; Waxman, 1957; Vegis, 1964).

Wareing (1951) reported that there is no evidence that spring breaking of dormancy under natural conditions is photoperiodically controlled, for dormancy is readily broken at any time from January onward by exposure to warm conditions, regardless of the length of the photoperiod. Thus, although chilling is required to overcome dormancy, by January or February the plants have changed from innate dormancy (rest) to imposed dormancy (quiescence) and the actual time of bud break is determined by rising temperatures in the spring (Wareing, 1969). Smith and Kefford (1964) concurred in stating that the major factor in controlling the initiation of spring growth is rising temperatures. They recognized three phases of dormancy: (1) dormancy development leading to the dormant state; (2) release from dormancy to a nondormant state; (3) the initiation of the spring burst of development. They further stated that following suitable chilling plants may be released from dormancy but may show no growth if a suitable environment is not provided.

At the time of maximum growth activity, usually only a short time after completion of the rest period, buds are able to break over a wide range of photoperiods or often completely independent of the daylength. However, after a period of time, a photoperiodic requirement for the continuation of growth may develop. The temperature during the daily dark period is very important, often decisive for the growth response of plants to the photoperiod (Vegis, 1964).

Many researchers have speculated on the necessity for a chilling requirement to facilitate normal budbreak in the spring. Several workers have confirmed a reduction in the level of endogenous inhibitors in the buds of woody plants during the course of the rest period (Wareing and Black, 1957). Perhaps the effect of low temperatures is to reduce inhibitor levels or to remove a block to gibberellin bio-synthesis leading to dormancy removal (Eagles and Wareing, 1963; Smith and Kefford, 1964; Wareing and Saunders, 1971; Bachelard and Wightman, 1974).

Photoperiod, Temperature and Latitudinal Effects on the Induction of Dormancy

In general, it has been reported by many researchers that short days cause cessation of growth and hasten the onset of dormancy (cessation of shoot growth, formation of resting buds) and long days delay or even suppress the normal onset of dormancy in the fall and promote bud break in the spring (Wareing, 1949a, 1953; Pauley, 1957; Downs and Borthwick, 1956; Vegis, 1964; Wareing, 1969; Weiser, 1970). More correctly, it is the length of the dark period that is important in dormancy induction (Wareing, 1953). This was shown by subjecting plants to a long night, which caused dormancy induction. However, if a light break was given in the middle of the long night, the plants behaved as if in long days. Thus, the important factor was the length of the unbroken dark period (Vegis, 1964).

Giertych and Farrar (1961) tested jack pine in five levels of nitrogen and two photoperiod levels, one with a light break in the middle of the dark period. They found that, with the break, plants doubled in height, dry weight and leaf weight, with increased root weight and delayed dormancy as compared to plants with an uninterrupted dark period. Neinstaedt and

Olson (1961) described the growth in these treatments as a response to a "critical night length." Several workers have experimented with the relationships of photoperiod and temperature by means of growing plants under one set of conditions and then transferring the plants into a new environment. Thus, Downs and Borthwick (1956) found that when several species of woody plants were transferred from long days into short days, most species required about four weeks of eight-hour days after transfer before they ceased growth. At higher temperatures, the delay period for red maple was significantly longer until bud set. Wareing (1956) also found that increased temperature delayed the onset of dormancy in short days for very young birch seedlings. In another example of a high temperature inhibition of a short day response, Patton and Willing (1968) grew hybrid poplars in nine different temperature and photoperiod combinations and found with the highest temperature treatment (33/28^{o} C) plants did not set bud even in the shortest (eight hour) photoperiod. VanderVeen (1951) found that when poplars grown under long days and short days were abruptly placed in short days (nine hours) at 5^{o} C, the plants previously grown in short days at higher temperatures dropped their leaves, while those plants grown in the longer photoperiod retained theirs firmly. Even after three months of artificial winter, most of the leaves were intact. After three months in the cold, plants were returned to their previous environments. Those in long days (16 hour) and continuous light immediately resumed growing, so apparently dormancy was not induced by the three months at 5^{o} C. Those plants in the shorter photoperiods (12 hour, 9 hour) took several weeks to resume growth. Plants that had set bud in short days only a few days before were placed in a long day environment; they resumed growth immedi-

ately, suggesting that the state of dormancy increased during the period when growth had stopped but the leaves were on the plants and were exposed to short days.

With some woody species, when the day-length exceeds a certain "critical" value for that species, growth may be maintained continuously throughout the winter. At day-lengths below this critical value, the duration of the growing period increases as the length of the daily photoperiod increases (Moshkov, 1930, 1932; Wareing, 1949a), or more correctly, as the length of the dark period shortens (Nitsch, 1957a). In the shortening days following the summer solstice, the photoperiod falls below the critical value, resulting in the cessation of growth and induction of winter dormancy in many woody species (Pauley, 1957). This critical value should not be confused with the "critical day-length" needed to promote flowering in herbaceous plants.

Photoperiodic control of the cessation of extension growth under natural conditions has been shown for many species (e.g., Populus triccocarpa, Pauley and Perry, 1954). With the addition of supplementary light, these plants grew until the temperature became limiting (Kramer, 1936). On the other hand, tree age may have an effect on the response of the tree to photoperiodic stimuli. For example, Wareing (1969) states that many species of older trees cease extension growth in June, July and August when day-lengths are long. Wareing states that it is unlikely that declining day-lengths play a major role in determining the duration of extension growth in mature trees of most woody species. Soil, water and nutrient levels may be adequate and available but Wareing feels the most probable cause of early cessation of extension growth may be internal competition for nutri-

ents within the tree. Even in cases where shoot growth continues until the short days of autumn (e.g., Populus), it is possible that seasonal factors other than photoperiod may be involved. Wareing (1949b) and Wareing and Saunders (1971) stated that other factors such as water stress or nutrient limitations may override the photoperiodic control of dormancy in some species causing the formation of quiescent buds which are subsequently transferred into fully dormant buds under the influence of short days.

Although height growth is determined by the interaction of hereditary potential and environmental factors, Kozlowski and Ward (1957) stated that the length of the growing season and shape of the growth curve of a species are apparently controlled mostly by hereditary factors and appear to be relatively independent of the normal fluctuations in the environment. Severe drought or low temperature may check height growth somewhat but the usual variations in water and temperature apparently have little effect (Kramer, 1943).

Hoffman (1953) grew Populus spp. from varying provenances both in the field and in glasshouses. He found that hybrids with the same female but different male parents had different reactions under the same day-length. He suggested that this showed nuclear inheritance and that responses to photoperiod were genetically controlled.

It is important to recognize the interactions of temperature, photoperiod and dormancy when transferring seedlings out of their natural range. Vaartaja (1959) stated that the farther north the origin, the greater is the photoperiodic sensitivity and the longer is the "critical" day-length. Vaartaja (1960a) stated that the longest inhibitory ("critical") day-length was correlated with the latitude of the seed source. At northern high

latitude sites, a long day photoclimate still exists when the temperature is cold enough to require dormancy. When trees adapted to this site are transferred south into shorter days, the result is early dormancy although the temperature may be favorable for growth. Conversely, when trees are transferred northward, they incur frost damage, due to the fact that at the original site they have become adapted to be in full growth under the long northern photoperiod that prevails even when winter cold or early frost starts at the new site (Nienstaedt and Olson, 1957; Vaartaja, 1959). Thus, these transferred species lack the proper timing of cold acclimation to survive (Weiser, 1970). Therefore, the ability of woody species to perceive photoperiodic stimuli is important in order for the species to become adapted to the natural environment. In the temperate regions, the duration of the frost free period is a major factor in the environment and limits the period of active growth. Since trees are more resistant to frost damage in the dormant condition, it is clear that the time of onset of dormancy may play a critical role in determining whether a given species can survive under various climatic conditions (Wareing, 1949a). This is important even for species in which seasonal growth is controlled endogenously, because even here the duration of growth increases progressively with the length of the photoperiod. Here the duration of seasonal growth is controlled by the genotype as well as by the sum of the environmental factors, including photoperiod. Vaartaja (1962) stated that growth and dormancy alternation are determined by temperature, photoperiod and endogenous interactions and that these responses may vary from one biotype to another. He further stated that northern trees of Betula, Picea and Larix possess

both an endogenous rhythm and a photoperiodic response which can overrule the rhythm.

Pauley and Perry (1954) state that the role of photoperiod in the annual growth cycle of Populus spp. appears to be primarily effective in the timing of the physiological p. .esses concerned with the onset of dormancy. In an indirect way, the photoperiod response enables the tree to utilize the warmth of summer and to protect itself from the cold of winter. Generally speaking, there is a close relationship between the photoperiodic conditions and the length of the warm season, so it is understandable that trees grown in the same photoclimate but in different thermoclimates react differently to various photoperiods.

Perry (1953) suggested that in response to the selection pressure of seasonal variation in temperature, poplar tree species have evolved a genetic system to control their duration of seasonal growth and initiation of frost resistance. Photoperiod, the only factor of the environment with a uniform seasonal variation which is constant from year to year, is the factor which evolutionary pressures have selected as the dominant agent for controlling duration of growth and frost resistance. The indirect adaptation of trees to the temperature conditions by means of the photoperiod offers a special advantage to the trees. Natural selection in a tree population may not take place under the control of the temporarily variable thermoclimate as much as under a more general and stable factor, the photoperiod (Vaartaja, 1954, 1959, 1960a; Irgens-Moller, 1957).

In a set of experiments done by Van Huystee, Weiser and Li (1967), plants subjected to decreasing photoperiod alone, with temperature constant, did not appreciably acclimate to cold temperatures imposed later;

those subjected to decreasing temperature alone, with photoperiod constant, acclimated only slightly. When the rest period induced by short days preceded exposure to gradually decreasing temperatures, the cold acclimation was rapid and substantial.

Hellmers (1959) cited an example of this in reference to Coulter pine and Douglas fir. Extended warm periods frequently occur during the winter months followed by freezing temperatures. However, the buds are prevented from opening until March or April when the danger of frost is past by the length of the photoperiod. Similarly, Vaartaja (1956) reported that photoperiod influenced the germination of seeds. Long days were positively correlated with a stimulation in germination of Betula seeds. This agrees with work done by Black and Wareing (1955). Ecologically, photoperiodic control over seed germination is probably important in keeping freshly fallen seed dormant until favorable temperatures (and long photoperiods) occur in the spring.

Controlled Environment Research

Definition of terms

Before discussing the particulars of controlled-environment research, it is necessary to define the types of physical structures that may be used in this type of work. Hudson (1957) suggested several factors that help to define and differentiate these facilities from one another. Growth cabinets are sealed structures in which plants can be grown under either natural or artificial light. These structures are not large enough to admit the operator. Growth rooms are structures that are artificially lit with sufficient light intensity to enable plants to make more or less normal

growth for prolonged periods of time. These rooms are large enough to permit the operator to enter them. Generally, there is more flexibility, at higher cost, than with growth cabinets. Temperature control rooms are large areas with relatively low light intensities. The largest controlled environment installation is the phytotron. This is a complex, including a series of growth rooms, temperature control rooms, growth cabinets and glasshouses, situated at one site (Hudson, 1957; Carpenter, 1966); a true phytotron permits control over most main environmental factors including humidity. The experimenter can deliberately change environments and is able to differentiate and integrate the action of the individual environmental conditions (Hudson, 1957; Went, 1963; Lange, 1963). Hudson proposed that the term "growth-chamber" be dropped in reference to environmental control, because the term has been used indiscriminately in the literature to refer to installations ranging in size from small cabinets to large rooms. In the context of this paper, I will use the term "growth-chamber" to mean the same thing Hudson defined as the growth cabinet, with the exception that natural light conditions were not available within the chamber.

Growth chamber environment vs. field environment

Many researchers have indicated that extrapolation of growth chamber results to field conditions involves several areas of concern. Principally, the concern is in relation to the differences in environment between the two.

Evans (1963) stated that plants in the field grow under conditions which are constantly changing, in microclimates which are spatially diverse

and in communities in which individuals may interact with one another. Evans contrasted this environment with the one in a controlled environment, where plants are grown under conditions which are stable in time, spatially uniform, and free of marked interactions with one another. Carpenter (1966) stated that most natural environments tend to fluctuate widely and any predetermined environment is artificial since it can only approximate to a condition or a combination of conditions that exists periodically in a natural climate. Langridge (1963) cautioned that the natural climate fluctuates both randomly and cyclically and that these shifts have been historical components in the experience of the genotype. Thus, their influence will be reflected in the behavior of any given genotype in a suitable set of controlled conditions. Vaartaja (1959) stated that the stable conditions in controlled environments never occur in the complex natural environment, which changes both cyclically and irregularly. Evans (1970) reminded researchers utilizing controlled environments that complex interactions, continued and rapid changes and marked gradations are realities of the field and that limitations on the ability to take into account all of these complications in a model must always limit the accuracy of extrapolation from controlled environments to the field. Hamner (1963) concurred with this when he pointed out that the tendency of experimenters is to keep all factors at a constant level except the one under experimentation and thus attribute the experimental results to the single variable; however, plants have evolved on the surface of the earth under constantly changing conditions with regular diurnal variations. Constant conditions, therefore, are alien conditions and may lead to abnormal plant development.

Thorne (1970) stated that results from studies where the controlled environment remained constant during the experiment are of limited relevance for models of growth and photosynthesis in the field unless the response to changing a particular environmental factor is known to be unaffected by previous conditions. Went (1963) discussed these ideas in terms of work on the circadian rhythm in tomato plants. He stated that one cannot properly measure development under completely constant conditions in growth chambers since the reaction system requires a circadian rhythm to react normally. Weiser (1970), in relating work on cold hardiness, pointed out that one of the main interests of the research was to discover the processes for inducing cold hardiness at will under controlled conditions. Weiser suggests that this is not possible because of the cyclic internal factors: for example, during the spring flush of growth, many plants will not acclimate fully regardless of the regimes of the photoperiod and temperature. On the other hand, these plants acclimated to some extent at the end of the growth cycle in the autumn even in supplementary long days and high temperatures in the greenhouse. Weiser suggested this behavior could be explained in terms of hardiness rhythms associated with the cessation of growth and physiological age of the plant or with seasonal environmental stimuli other than the temperature or photoperiod. DeVries (1963), in relating the results of experiments conducted in a phytotron to conditions found or obtainable in the field, said one could legitimately ask how the artificial environment compared with a natural or modified natural one, i.e., how the various physical, chemical and biological factors in the controlled and uncontrolled environments compared. In this sense, a modified

environment was one that was changed to a large extent by cultural measures, for example, irrigation, shelter or application of nutrients.

Several writers have written in reference to specific climatic differences between the controlled environment and the field. Bunting and Cartwright (1957) and Evans (1963) pointed out that the fluctuation of aeration and carbon dioxide content of the field soils was very different from those found in the constant confines of a pot. Gaastra (1970) stated that the generally low wind velocity in growth chambers could result in high and variable mesophyll resistance (ra) values, which for upper leaves may exceed the values found in the field. Similarly, Ludlow (1970) suggested that wind speed at the top of a vegetative canopy in the field might be much higher than those found in growth rooms while those at the base might be much lower. Lake (1970) stated that, even in artificially illuminated growth rooms, the rate of carbon dioxide uptake may vary during the day; therefore, constancy of illumination does not guarantee constancy of the rate of carbon dioxide uptake.

Other factors that have been contrasted between the field and controlled environments are soil properties, such as temperature, acidity (Evans, 1963, 1970; Bunting and Cartwright, 1957; Hudson, 1957; Wassink, 1957), humidity (Bunting and Cartwright, 1957; Evans, 1963), weeds and pests (Bunting and Cartwright, 1957; Wassink, 1957; Evans, 1963), rates of evaporation (Bunting and Cartwright, 1957), diseases (Bunting and Cartwright, 1957; Evans, 1963), polluting agents (Evans, 1963, 1970) and population density (Wassink, 1957).

Temperature changes markedly in the field, whereas it is usually held constant in controlled environments (Bunting and Cartwright, 1957; Evans,

1963; Wassink, 1957). Evans (1963) further stated that the temperatures of the plant leaves themselves may be quite different in the field and in the growth chamber.

Water and nutrient differences can also be found between the two environments (Bunting and Cartwright, 1957; Evans, 1963; Wassink, 1957).

One of the main environmental components different between the field and artificially lit growth chambers is light quality and quantity. Thorne (1970) found that plants growing in growth rooms having temperatures similar to those found outdoors differed from the field plants in ways that seemed to depend on the differences in light quality rather than on differences in light intensity. Thorne (1970) cautioned that if results from experiments in controlled environments are to be incorporated into models of field growth, it is important to test that the responses to changing climatic factors in the artificially lit growth chamber also occur in natural light in the field.

Wareing (1956) pointed out that the demonstration of photoperiodic responses in relation to experimentally controlled day-length and light conditions does not imply that such effects will occur in nature.

Other workers have emphasized the differences in light environment between the growth chamber and the field. Lake (1970) pointed out that in the field there was no variation of illumination with height in the part likely to be occupied by plants, whereas in the growth chamber the illumination at the floor level (112 cm from the ceiling) was only 75% of that at the top. Furthermore, maximum illumination in the growth chamber was only 30% of that in the field. Hudson (1957) concurred with this and stated that the ideal growth chamber would have a uniform arrangement of illumina-

tion and that the researcher should vary the plants in the chamber as they increase in height between the light source and the upper surface. Evans (1963) further stated that, in the field, competition for light, water and nutrients in plant communities may be severe enough to reduce the importance of other climatic responses. Vince and Stoughton (1957) said that the common practice of exposing plants to irradiations whose intensities are measured in terms of foot-candles, lux, lumens/square foot or similar subjective units leads to invalid comparisons except where the sources are of identical spectral composition.

Aside from the fact that there are considerable climatic differences between controlled environments and the field, Bunting and Cartwright (1957) stated another reason to restrict the application of controlled environmental research. They pointed out that there are instances where the apparent physiological optimum (which may have been found using controlled environment) does not coincide with the ecological situation in the field. They suggested that researchers should not be concerned with securing the optimum conditions for individual plants growing in an agronomic mode, because the goal of maximum yield per acre is achieved only under conditions of intense inter-crop competition. In other words, they felt that using controlled environments to select for superior yielding plants was not of value, because under field conditions the total yield is obtained at a very low level of yield per individual plant. However, these authors were primarily concerned with grain yield (e.g., sorghum) and not with fiber yield.

In conclusion, when the temperal changes and spatial diversity of natural microclimates are compounded with the complexity of interactions

between environmental factors and between plants growing together, the prediction of performance in the field from that under controlled conditions may seem an impossible task. Certainly prediction of total field performance is still beyond researchers (Evans, 1963).

Uses, Purposes and Objectives of Controlled Environmental Research

According to Carpenter (1966), three criteria appear to be important in defining the ideal growth chamber: conditions should be uniform in space and time, conditions should be defined and reproducible and plants grown in the controlled environment should not be too dissimilar from ones grown in a typical natural climate.

A controlled environment meeting the above three criteria is invaluable for many types of research on plants. Facilities for controlling specific climatic factors can be used to gain an understanding of the plants' response to the field environment. In the field, components such as temperature, day-length and light intensity are confounded and it is difficult to isolate the contributions made by one factor; weather is infinitely variable, unpredictable and complicated. In a controlled environment chamber, it is possible to study the response of plants to a particular set of conditions (although not necessarily natural) because it is possible to vary independentally climatic factors one at a time (Thorne, 1970). The greater the range and the number of environments available, the more effectively this can be done (McWilliam, 1966; Hudson, 1957).

Thomas (1957) cited two important advantages in using controlled environments to study plant growth in this way: (1) the effects of genetical differences can often be increased or even revealed for the first time

under appropriate controlled environmental conditions and (2) when genetical studies are carried out under these conditions the physiological implications of the underlying genetical differences can be fully investigated.

Nelson (1963), for example, suggested that as plant physiologists turn more and more to work in controlled environments, it will become possible to appreciate the magnitude and site of action of the many internal and external factors that affect such physiological processes as translocation. He stated that under growth chamber conditions, it is not uncommon to observe large differences in morphology and translocation. He showed that as light intensity increased within controlled environments, wheat data showed a steadily increasing amount of assimilate being translocated to the roots, resulting in an increased root-shoot ratio. By virtue of controlled environment conditions, researchers are able to study these physiological changes with varying environmental conditions.

Langridge (1963) stated that patterns in genotype-environment interactions may be more readily discerned by observing the expression of complex genotypes in simplified environments rather than by studying mutationally altered genotypes under uncontrolled conditions.

Besides distinguishing between the effects of closely related environmental factors on plant growth, controlled environments can also be used to show how the response to a particular environmental factor depends on previous history. For example, the artificial climate can be changed at various times during the growth period or at specific growth stages (Thorne, 1970). Particular phases of growth can be shortened or lengthened; for example, particular combinations of temperature and photoperiod can be used to induce flowering by breaking dormancy, satisfying vernalization require-

ments or by photoperiodic induction, and thus the generation interval can be effectively shortened (McWilliam, 1966). Controlled environment can also be used to synchronize flowering of different genotypes to achieve hybridization. This has definite advantages in breeding research (Hudson, 1957). Through the use of controlled environment chambers, "seasonal" changes can be made at will and experiments can be carried out at any time of the year. Stress conditions can be provided at will to screen out varietal response to certain sets of conditions, whereas in nature it might take years for the appropriate conditions to occur (Hudson, 1957).

Controlled environments are also a useful tool for investigating the influence of various climatic factors on the relationship between photosynthesis, growth and economic yield. Environmental factors may affect yield via the size of the photosynthetic system, the rate of the photosynthetic system or the capacity of the storage organs to accumulate carbohydrates (Thorne, 1970). Experiments in controlled environments can help to establish the relative importance of these processes in contributing to yield when a particular environmental factor is altered.

It is possible that the effects of weather on photosynthesis and growth can be studied during short periods in the natural environment by calculating multiple regressions of growth attributes on environmental factors but this technique is very insensitive because different environmental factors are often highly correlated in their seasonal variation (Thorne, 1970). Results from controlled environment studies can be compared to field studies using regression techniques, however. Welbank et al. (1968), studying wheat, found that the independent effects of radiation and temper-

ature on yield shown by regression analysis were real and that the extrapolation from the controlled environment to the field was justified.

Lange (1963) suggested that controlled environment apparatus is valuable in studying the heritable carry-over effects of various environmental treatments. For example, it was found that the temperature that seeds were germinated at had a carry-over on plant dry weight size after eight days in a controlled environment of one temperature and photoperiod.

Another use for controlled environments involves the production of uniform plant material. Biological material is inherently variable; anything to reduce the variability between plants greatly facilitates research by reducing the number of replications needed to show significant results and thus enables experimental layouts to be simplified (Hudson, 1957). Growth chambers can be used to eliminate some of this variation.

McWilliam (1966) suggested that controlled environment facilities had a main role in plant improvement research. He suggested that they should be used as a diagnostic tool to help isolate and identify the most important climatic factors responsible for disease and weakness in plants. Controlled environments enable researchers to grow plants over a wide range of environments and thus determine the adaptability of the material. McWilliam (1966) cautioned, however, that information gained from this type of study does not permit one to predict accurately the particular climate in which the plant is most likely to succeed; one is more likely to pick the environment in which the plant will not succeed. Andrews (1958) concurred with this and stated that when dealing with entirely new crops or with plants introduced of unknown performance, controlled environment studies should at least predict where they will not succeed but also may

give fairly specific clues as to where they will succeed. Leibundgut and Heller (1960), in a provenance study from Switzerland, found that rapid tests by exposure to varying temperatures or light intensities could reveal considerable differences in provenances even within a small area. Tests of this type with unknown material could be used to match particular genotypes with optimum environments. With introduced plants, one may not be so interested in prediction of its likely adaption but may wish to examine the reaction of certain ecotypes to components of the environment with the view of revealing particular responses which may be of value in a breeding program. For example, Kramer (1936) suggested that knowledge of the optimum photoperiod for a certain species should aid in predicting whether or not a given species is suitable for growth at a given latitude. Similarly, Hellmers (1967) tested sequoia and Pinus engelmannii to find the optimum range of temperature conditions for maximum survival and growth. Using controlled environments, he found that night temperature was more important than day temperature in controlling growth. Lange (1963) also reported on work done to examine the relationships of growth and temperature. He found that in some species (loblolly pine, Douglas fir) the effect of temperature on growth was determined mostly by the differential between the day and night temperature. In other species, growth was controlled by the day temperature (redwood), the night temperature (digger pine) and by the daily heat sum (Jeffery pine).

Andrews (1958) further suggested that with an established crop, the most profitable approach might be to examine the climatic control of the physiological processes limiting production. In some cases, the limitation may be survival after extremes of heat or cold; in these cases, performance

under controlled conditions can be highly correlated with that in the field.

The ability of controlled environments to provide stress conditions may be helpful in plant breeding programs. The expressions of variation are often masked at or near the optimum conditions for growth. By exposing plants to various environmental stresses, at or near the limits of tolerance, new and useful latent variation may be revealed (McWilliam, 1966). The development of many plants in the field may be limited by a single environmental factor, such as photoperiod or temperature; by defining these particular factors responsible for limiting growth, breeding programs may be tailored to overcome these limitations.

With plants from closely related populations, growth characteristics are often less distinct and genotype-environment interaction may be of greater significance than when dealing with plants from extreme population differences. The complex nature of the field environment suggests that population-environment interactions may be resolved more readily under controlled environment conditions, where it is possible to vary climatic components such as photoperiod and temperature individually (Bunting and Cartwright, 1957; Broue et al., 1967). These workers found, by examining growth responses to regimes of two photoperiods and two temperatures, that plant growth varied markedly under different photoperiods and that the magnitude of the differences increased with increasing temperature.

Use of Controlled Environments for Rapid Selection

Nienstaedt and Olsen (1961) stated that field testing will always be a part of seed source studies and that field progeny tests of forest tree

ecotypes are necessary to assess the ultimate value of the various genotypes of trees. They stated, however, that certain types of racial variation may be studied at the seedling stage by growing the plants under artificially controlled environments. For example, these workers exposed various collections of Jack pine from widely different provenances to long and short photoperiods. They expressed confidence in the feasibility of these tests to select for those populations that might grow best in certain field locations, although they emphasized that conclusions from growth chamber experiments must be applied with caution to field situations.

Tests of this type may give an indication of the response of the plants to particular environments and may show the amount and type of genetic variation within a species. Using controlled environments, the separate effects of heredity and environment can be studied and their interactions shown in a way that is not possible in the field.

Callaham (1964) stated that extrapolation from the results of seed source tests would have been most efficient if biosystematic investigations had been done. This involves the use of data from ecological and physiological studies, measured on plants growing under both artificial and natural environments. Callaham further pointed out that growing plants under controlled environments permits an assessment of heritability of characteristics and the interaction between genotypes and phenotypes and the environment. He further suggested that particular emphasis should be given to studying the nature of the photoperiodic control of growth.

McWilliam (1966) felt that the provisions of standard, reproducible environments would be of great value in reducing the environmental variation and increasing the precision with which one could estimate the genetic

composition of unknown variaties. For example, Hermann and Lavender (1968) collected seed from 14 sources of different altitudes and aspects and grew them both in the nursery and in growth chambers. Not only did growth rates decrease with increasing altitude of seed source but the growth differences between aspects were most clearly seen in the growth chambers; plants from S facing aspects had a shorter growth period with lower shoot to root ratios. The authors pointed out the value of observing the material under controlled environments when they stated that dissimilarities in the nursery environment seemed to mask genetic differences.

Yeatman and Holst (1967) stated that estimates of genetic variability could be obtained from tree seedlings grown in a uniform environment. They pointed out that if sound prediction of adult performance could be made from short-term tests, large numbers of seedlings and seedlots could be tested under standard conditions and only relatively few selected lots would need be carried forward for long-term testing in the field. These researchers correlated the dry weight of four-month-old seedlings of Jack pine grown in controlled environments and glasshouses with the height of the same populations grown for three and four years in the field for 38 provenances extending over a wide range. Although only one combination of photoperiod (15 hours) and temperature (21/13^{o} C) was used, correlation values of the performance of the seedlings at different ages were highly significant ($r = 0.86$). However, the efficiency of selection at an early age for high performance at a later age (based on relative rankings) was only moderate. Lower efficiency may have been caused by the high variation in both the plant material grown in the growth chamber and the large variability in the site quality of the field test location. These workers con-

cluded that early tests in controlled environments could be of value in screening genetic material for potential growth.

Cameron (1967) experimented with collections of Townsville leucerne from widely different locations with reference to flowering time. He felt that by using controlled environments to vary combinations of temperature and photoperiods, knowledge of the factors controlling flowering could be obtained and that this data might explain the natural distribution of the species and assist in selecting strains for growth in different environments. They concluded that although extrapolation from the controlled environment to the field is generally difficult, confidence could be placed in predictions of "earliness" or "lateness" based on flowering time studies in response to given climatic conditions.

Giertych and Farrar (1962), using plants from northern and southern provenances, found that total dry weight, height and leaf and root dry weight were all positively correlated with the number of degree-days (base 42° F) associated with the seed origin. Similarly, Yeatman (1965, 1967, 1974) studied the effect of the interaction of genotype and environment on seedling growth in growth cabinets and in the field. He found that the photoperiod had more effect on growth than the temperature but that the temperature was more important in controlling bud break. Overall, provenances differed in mean performance and in response to photoperiod but the effect of temperature contributed little to provenance differentiation. Using a number of climatic variables, taken alone and in combination, the authors found that the number of growing degree-days best accounted for variation in response among seed sources. Discrimination was made among the provenances by means of multivariate analysis. Yeatman further

reported that the patterns of response in the field paralleled those seen in comparably controlled environments in the growth cabinets. The analysis demonstrated an overall clinal pattern of genetic variation due to environmental adaptation. Langlet (1959) related growth variation to the annual periodicity of the temperature (number of days over 6° C in the native habitat of the provenance) and the daily period of day-length (day-length on the first day of the year when the mean temperature equaled 6° C).

Schmidt (1957, 1963) stated that to be effective predictions must be based on sufficiently high correlations between juvenile and adult characteristics. He stated that correlation coefficients should approach or exceed 0.80, the standard error of prediction should be low and the sample should be representative of the material being studied.

Selection Based on Field Observation

Various researchers have attempted to correlate the growth of seedlings at an early age with the final growth at some older age. Mohn and Randall (1971), using 38 poplar clones, found that height and diameter correlated both genetically and phenotypically; correlations between measurements in the first three growing seasons and those made in the sixth year were high. Growth was reported to be slower than usual due to the low site quality of the test site. However, based on these correlations, these researchers suggested that culling after two growing seasons was feasible. The authors cautioned that the correlation values calculated referred only to a particular population under particular circumstances and that the growth estimates should be most useful when applied to similar populations growing under similar site conditions. Rovskij and Sarkisova (1969), how-

ever, also reported of observations made on Populus hybrids and suggested that selection for growth rate should not be done earlier than age three to four years and that final evaluation could not be made until age 10-15 years.

Wareing (1956) suggested, since the period of seasonal extension growth is much shorter in mature trees than in the seedling stage, that conclusions regarding mature trees cannot be arrived at by extrapolation from the photoperiodic behavior of the seedlings. Kramer (1943), however, reported that the growth patterns of two-year-old seedlings of loblolly pine were very similar to the growth patterns of 13-year-old trees. Further, Kozlowski and Ward (1957) related a study showing that three-year-old hemlocks had a growth pattern similar to eight-year-old trees.

Kriebal (1962) established correlations between two- and nine-year-old heights in sugar maple from various seed sources. He concluded that although significant correlations were found, evaluation of vigor at age two was not very reliable. He suggested that other more highly heritable characteristics such as drought resistance, tree form and length of growing period could be estimated with considerable accuracy at an early age.

Webb (1963) concluded that characteristics exhibiting strong parent-offspring heritability could be selected for or against at fairly young ages and that other characteristics that were critical at an early age could also be evaluated early in the life of the population. Squillace and Silen (1962) emphasized the importance of uniformity of cultural treatments and accuracy of measurements of seedlings if such data are to be of predictive value. Using these criteria, they found highly significant correlations of 0.85 between heights of 2- and 50-year-old ponderosa pine. Holst

and Yeatman (1961) concluded that "few generalizations can be made concerning the predictive value of seedling studies for performance at an early age." They cautioned that each problem must be dealt with separately to determine the appropriate limits for selection.

METHODS AND MATERIALS

Field Study

In this study, three hybrid Populus clones, from southern Canada #5260 (Populus x tristis cv. no. 1), central Wisconsin #5377 (Populus x euramericana cv. Wisconsin no. 5) and central Iowa #5339 (Populus alba x grandidentata cv. Crandon) were used. Softwood cuttings of relatively uniform length and size were taken from stock plants growing in the greenhouse under a similar environment and were individually placed in commercially prepared Jiffy-7 peat pellets. These were then placed under an alternating mist system on greenhouse benches. When the roots emerged from the pellets after about three weeks, 45 of the plants (15 of each clone) were planted in 3 x 3 Latin square designs, with four foot by four foot spacing at each of two latitudes, the State Nursery (1971, 1972) or the Hines biological study area (1973), both near Ames at latitude near 42° N, and the Hugo Sauer Nursery in Rhinelander, Wisconsin, at latitude near 45° N. Three degrees difference in latitude was enough to give different environments and hence different growth patterns were expected. High levels of moisture and nutrients were maintained at both locations.

Measurements of stem height, taken from the top of the Jiffy-7 pellet to the top of the apical bud, and leaf number counts were made every two weeks following the planting time, which was the first or second week in June for all three years at both locations, with the exception of the July 1st planting date at the Rhinelander site in 1971. In addition, at approximately 30-day intervals (July, August, September), a destructive harvest was made of one randomly selected Latin square and measurements were taken

on the following variables in the stated fashion: (a) stem height, measured with a meter stick from the base of the stem, which was severed with a knife at the point of the uppermost lateral root (this point was located after the Jiffy-7 pellet had been removed); (b) stem diameter, measured at the base of the stem at the widest part with vernier calipers; (c) stem dry weight, measured after the stems were cut up and individually placed in paper sacks and dried for two or three days at 80° C; (d) branch dry weight; (e) leaf number, counted as all leaves greater than two centimeters in length; (f) leaf dry weight; (g) total top dry weight, found by adding the dry weights of stem, branch and leaves; and (h) leaf area, measured as follows: leaves were placed on paper, flattened with glass and then the paper was exposed to bright illumination and placed in crispers containing a small beaker of ammonia. Area was then calculated from the leaf imprint with a dot grid or an electronic planimeter. Results from both methods were comparable; a total plant leaf area was determined. The procedures outlined were repeated for the years 1971, 1972 and 1973 at both locations.

Plants that were not harvested during the first year were left at the site for additional measurements. These included measurement of stem heights every two weeks in the field at both locations. In addition, Latin squares were again harvested at the end of the growing season and the variables were measured as before. This was done for both second and third year trees from both locations.

Controlled Environment Study

For the controlled environment study, the same three clones were used and were propagated as in the field study. When the roots emerged from the

peat pellets, they were individually planted in black one-gallon (eight-inch) pots in a 1:2 mixture of perlite and Jiffy mix (sphagnum peat and vermiculite) plus a small amount of Magamp, a slow release fertilizer. Pots were then transferred into Model 80 P-T Percival growth chambers and placed in randomized 3 x 3 Latin square designs. Photoperiodic treatments were either 13, 14 or 15 hours; these photoperiods were chosen to cover the range of those naturally found during the growing season in the field at both locations. The photoperiod at Rhinelander is 15 hours on July 23, 14 hours on August 18 and 13 hours in Ames on September 3 (List, 1966). Experimental photoperiods were randomly assigned to chambers for each replication. Thus, 27 plants (3 plants/clone x 3 clones x 3 photoperiods) were used for each replication. Day temperature was maintained at 25° C and night temperature at 15° C based on work done with the Crandon clone (Domingo and Gordon, 1974).

Plants were fertilized once weekly with a commercial, water soluble, 20-20-20 fertilizer. One and two-tenths gram of fertilizer and three milliliters of EDTA (15 ppm Fe) were added to one liter of water and 250 milliliters of the combined solution was given to each plant. Plants were watered as necessary and pots were flushed with water at weekly intervals to prevent salt accumulation.

Measurements of stem height and leaf number were taken at approximately four-day intervals until the end of the experiment, when all plants were harvested and measured as in the field study. This portion of the study was replicated four times, with a total growing period being either six weeks (one time) or seven and one-half weeks (three times).

Light intensities varied somewhat in the chambers but averaged approximately 2,600 foot-candles at the apex, with a range of from 2,200 to 2,800 foot-candles.

Humidity was not directly controlled and varied depending on the frequency of watering.

Data Analysis

Analysis of variance was used to detect clone and location differences. Sources of variation examined were harvest, rows, columns, clones, harvest x clone, regression and error. Data for all variables from harvests for three years at both locations were analyzed. Tests of significance were made by comparing F-values at the .05 and .01 probability level. Means for harvest data (both first year and second- and third-year-old growth) were also calculated by harvest, clone and harvest x clone for each variable.

Analysis of variance was also used to test data acquired from bi-monthly measurements. This was done for all three years for both locations (except where data were missing from the 1971 Rhinelander site). Again, significance was tested on both first year and old growth by means of F-tests. Means were also calculated on the bi-monthly data by time, clone and time x clone and differences were examined by F-tests.

Correlations were calculated between all variables measured within each field location and between the growth chambers and each field location by means of two separate but related methods.

Both methods fit regression lines and calculated the correlation values from those lines; however, one method fit just one line (all years com-

bined) with locations separate, whereas the other method fit lines for each year of field data but locations were combined in this analysis. Tests of significance were based on a "values of r and R table" for the first method and on F-tests for the second method (Steel and Torrie, 1960). Values for correlation coefficients were comparable for both methods. All data were analyzed using the Statistical Analysis System.

RESULTS

The results from this study are presented under three main headings: field growth, growth chamber growth and correlations between the growth chamber and the field growth.

Within the field growth section, results are presented for both harvest data and nondestructive bi-monthly measurement data taken from two locations: Ames, Iowa, and Rhinelander, Wisconsin. Three Populus hybrids were used in the overall study and measurements were taken on several growth variables.

Results based on harvest information taken over three years showed that, although there were differences both in rate and amount of photosynthate accumulation between years and locations, certain trends were consistent. Mean values, as well as simple ranking of clones based on growth performance, were used as a basis of comparison.

Clone 5377 ranked in first place at both field locations by the end of each growing season in all three years and clone 5260 usually ranked last for all variables measured. In general, growth trends were the same at both locations for the years 1971 and 1973; growth in 1972 differed from the other two years but differed in the same fashion at both locations.

In addition to harvest data on replications of one season growing material, measurements were also made on trees left in the field for two and three years at both locations.

Rankings of clonal performance based on results from the bi-monthly measurements of the same three clones made on both first year trees and older trees agreed with rankings based on harvest data. Bi-monthly meas-

urement data showed that differences in growth pattern occurred between locations, probably because of clonal response to photoperiodic differences between the two areas.

Results from the growth chamber studies are also presented as harvest and weekly measurement data. Differences in growth as indicated by the measured variables occurred with different photoperiodic treatments. In general, growth improved with increasing photoperiod. Rankings of clones in the growth chambers were consistent with rankings based on field measurements.

To quantify the relationships between growth room and field growth, correlation matrices were calculated by various methods. In general, larger correlation coefficients were obtained between field growth and growth under longer photoperiods in growth chambers. Differences occurred in the magnitude of the values of r between locations with larger mean r values being found between the growth chamber growth and growth at the Ames location.

Field Growth: Harvest Data, by Clones, for Ames First Year Growth

Clone 5260

Differences occurred between years with respect to the pattern of growth for many of the variables measured. For example, height growth in 1971 was much better at the beginning of the growing season compared to the 1972 season but by the time of the second harvest values for stem height were approximately equal for these two years. Values in 1973 were below those for 1971 and 1972.

By the second harvest date in all three years, 5260 had set bud and nearly stopped height growth, so values for the third harvest time were only slightly greater or equal to the second harvest values in all years. There were differences, however, in final (third harvest) heights between years: the average height in 1971 at the end of the growing season was 10% greater than that in 1972 and 29% greater than that in 1973.

The trend in average diameter growth was similar to the growth in height for all three years. By the time of the last harvest, the average diameter was about the same all three years, although there were slight differences in harvest dates (Tables 1, 2, 3). However, the rate of diameter growth varied among the different years. Trees in 1971 and 1973 had reached a maximum value by the time of the second harvest; those in 1972 showed a steady increase in size throughout the growing season, reaching a maximum value at the time of the third harvest.

Differences occurred between years in the rate of accumulation of photosynthate in the stem. Stem weight growth in 1971 was similar to height and diameter growth. Between the first and second harvests, stem weight tripled. With the setting of buds, however, stem weight increases ceased and second and third harvest values were approximately equal. In 1972 growth initiation was slow and stem weight values at the first of the year were low, as were average heights. By the second harvest, average stem weight had increased 11 times over that at the first harvest time; by the third harvest in 1972, stem weight had further increased to a value close to that observed in 1971. In 1973 the slowing of height and diameter growth was also reflected in a smaller increase in stem weight during the

Table 1. Means by variable, clone and harvest for the 1971 growing season at Ames

Harvest	Clone	Dependent variables[a] SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW[b] (gm)	LA (cm^2)	LF
1[c]	5260	52.8	0.252	3.71	2.69	6.40	462.3	24.6
	5377	58.8	0.275	4.16	2.81	6.97	581.0	30.0
	5339	34.0	0.196	1.72	1.05	2.77	169.7	10.7
2[c]	5260	65.4	0.412	7.11	7.81	14.92	680.0	37.0
	5377	104.3	0.497	17.56	11.54	29.78	2137.0	59.0
	5339	65.4	0.340	7.74	4.79	12.92	831.5	38.5
3[c]	5260	62.6	0.367	7.01	7.48	14.49	548.0	22.0
	5377	128.4	0.806	47.18	48.42	105.18	4771.0	91.6
	5339	101.2	0.485	11.70	14.10	25.80	1196.3	27.0

[a]SH = stem height, SD = stem diameter, LW = leaf dry weight, SW = stem dry weight, TTW = total top dry weight, LA = leaf area, LF = leaf number. The abbreviations will be the same on subsequent tables.

[b]Values for total top dry weights include branch dry weight on this and subsequent tables.

[c]N = 3 for all harvests.

second half of the growing season; values were lower than those for either 1971 or 1972.

Following the setting of buds, little or no increase occurred in leaf dry weights all three years, i.e., maximum values were generally reached by the time of the second harvest. Final leaf dry weights per plant in 1973 were slightly less than the average 1971 value and 70% less than the 1972 value. The decline in leaf number between the second and third harvest times in 1971 and 1972 was presumably due to differences in sampling.

Table 2. Means by variable, clone and harvest for the 1972 growing season at Ames

Harvest	Clone	Dependent variables SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW (gm)	LA (cm^2)	LF
1[a]	5260	12.6	0.246	1.08	0.38	1.46	165.7	16.3
	5377	31.4	0.252	1.75	0.67	2.42	358.3	22.0
	5339	15.4	0.139	0.26	0.22	0.47	75.5	12.0
2[a]	5260	61.0	0.332	9.01	4.46	13.84	1108.3	33.7
	5377	82.4	0.428	15.26	7.71	23.22	2098.5	50.5
	5339	24.9	0.152	1.45	0.35	1.80	104.3	11.3
3[a]	5260	56.7	0.346	9.99	6.90	17.81	965.3	27.3
	5377	103.8	0.654	22.69	23.62	47.59	2514.3	46.7
	5339	34.9	0.228	1.17	1.32	2.49	171.5	13.5

[a]N = 3 for all harvests.

Table 3. Means by variable, clone and harvest for the 1973 growing season at Ames

Harvest	Clone	Dependent variables SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW (gm)	LA (cm^2)	LF
1	5260	No trees harvested						
	5377	No trees harvested						
	5339	No trees harvested						
2[a]	5260	46.3	0.325	5.45	3.48	8.93	505.3	19.3
	5377	66.0	0.355	10.12	5.11	15.23	1256.0	31.0
	5339	18.8	0.187	0.30	0.51	0.81	40.0	3.0
3[b]	5260	48.5	0.325	5.86	5.14	11.00	580.0	21.5
	5377	121.7	0.666	31.12	39.00	73.53	2625.7	74.1
	5339	76.5	0.329	10.04	10.00	20.04	1044.8	29.6

[a]N for harvest 2 = 3.

[b]N for harvest 3 = 12.

Final leaf number was identical for the years 1971 and 1973, while values for 1972 were somewhat higher.

By definition, values for the total top dry weight variable were the summation of average stem and leaf dry weight; therefore, total top dry weight changes throughout the growing season paralleled changes in those variables.

Values for average total plant leaf area changed seasonally in a fashion similar to the other variables measured. In 1971 leaf area increased by almost 50% to a maximum value at the time of the second harvest. The average total plant leaf area value for the third harvest was lower than the maximum found earlier in the season. However, from examination of the average individual leaf area (total leaf area per plant divided by the average leaf number), it was seen that although there were significantly fewer leaves at the third harvest, in comparison with the second harvest time, the average leaf area steadily increased throughout the growing season.

Likewise, in 1972, the average total plant leaf area was greatest at the second harvest time and decreased slightly by the third harvest time. Again, however, the average leaf area increased slightly over the growing period.

In 1973 average total leaf area increased somewhat after the second harvest time to reach a maximum value at the third harvest. Average individual leaf area also increased in this growing season.

Rates of average total leaf area increase by years were similar to the increases in the other measured variables. For example, average total plant leaf area in 1972 increased over six times from a relatively low

first-harvest value reaching a second harvest value larger than that for the same period in 1971.

Values of maximum average total plant leaf area for 1973 trees were 91% lower than those for 1972 trees and also lower than those found in 1971. Final values (third harvest) for 1971 and 1973 were close; those for 1972 were much greater.

From examination of the average individual leaf area, it was seen that there were differences in allocation of photosynthate to leaf area expansion between years. For example, second harvest values for 1971 and 1972 showed nearly identical leaf numbers. However, average individual leaf area and weight were greater for the 1972 plants. Similarly, in 1973, the values for second harvest leaf number were considerably smaller than in 1971 but the average individual leaf area was slightly greater in 1973.

Clone 5377

Unlike 5260, clone 5377 continued to grow in stem height throughout the growing season in all three years. Differences were apparent both in total amount of growth between years and in relative rates of growth within particular years.

Trees in both 1971 and 1972 grew best in stem height during the first half of the growing season. Final heights were approximately the same all three years, allowing for differences in harvest times.

In general rates of diameter increase were similar in the first half of the season in 1971 and 1972 but because the rate of increase slowed down more in the second half of the 1972 season, final diameters were greatest in 1971. Although the average diameter was smaller in 1973 at the second

harvest compared to the average in 1971 or 1972, rapid growth in the second half of the season in 1973 resulted in an average diameter approximately equal to that attained in 1972.

Large differences occurred between years in stem dry weight. In 1971 stem dry weights increased by about the same magnitude (four times) between each harvest date. In 1972, however, stem weights were considerably smaller than in 1971 at the first harvest and large gains later in the season in 1972 still resulted in average stems that weighed only one-half as much as those attained in 1971. Stem growth in 1973 differed from the two preceding years in that second harvest values were less than one-half those found in 1971. However, the rate of stem weight growth in the second half of the 1973 season was almost twice that observed in 1971. Final average stem dry weights were only slightly less than those found in 1971 trees.

Rates of increase in leaf dry weight and number between the years 1971 and 1972 were similar to stem dry weight. Effects of harvest time, clone and the harvest time x clone interaction on leaf number were not significant at the 0.5 level probably because of the large variability in numbers about the mean and the relative smallness of the sample (Table 4).

In 1972 leaf weight, like stem weight, increased greatly (13 times) between harvests 1 and 2 but then made only modest gains in the second half of the season. Average leaf number actually showed no gain by the third harvest, even though the average plant height had increased markedly. Again, similar to stems, leaves at the third harvest in 1972 weighed only one-half of those measured in 1971. Leaf weights for 1973 trees were smaller than 1972 weights at harvest two but because they continued to grow

Table 4. Mean square values[a] by variable and year for first year harvest data at Ames

Source and year	DF	Dependent variables: SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW (gm)	LA_2 (cm^2)	LN
1971								
		<.01[a]	<.01	<.01	<.01	<.01	<.01	.16
Harvest	2	836.60	0.21	811.25	1077.50	4410.20	7057396.50	1524.70
		<.01	<.01	<.01	<.01	<.01	<.01	.07
Clone	2	381.80	0.06	560.25	481.95	2512.70	6920905.00	2359.20
		<.01	<.01	<.01	<.01	<.01	.01	.32
Harvest x clone	4	136.90	0.04	367.13	405.75	1969.10	7352784.00	1806.15
Error	8	6.43	0.03	35.84	10.88	134.60	5685805.50	647.65
1972								
		<.01	<.01	<.01	<.01	<.01	<.01	.03
Harvest	2	3982.88	0.07	200.03	197.87	773.04	2302478.92	422.58
		<.01	<.01	<.01	<.01	<.01	<.01	<.01
Clone	2	3172.09	0.12	196.80	147.65	712.04	3752633.90	1214.17
		.02	<.01	<.01	<.01	<.01	.05	.16
Harvest x clone	4	588.25	0.02	61.94	94.73	319.13	757756.50	160.86
Error	9	102.47	0.001	5.11	4.61	13.82	182618.30	70.70
1973								
		.01	.02	.05	.01	.01	.24	.06
Harvest	1	3609.36	0.07	290.82	743.38	2059.57	1127501.70	1003.11
		<.01	<.01	<.01	<.01	<.01	.02	<.01
Clone	2	4808.40	0.10	516.24	742.78	2723.62	4052381.98	2221.99
		.05	.02	.07	.01	.01	.58	.06
Harvest x clone	2	1574.26	0.05	219.93	553.68	1662.24	713343.92	788.32
Error	18	462.34	0.01	69.67	95.60	242.62	775083.99	246.51

[a]Superscripts associated with M.S. values are probability levels of significance on this and subsequent tables.

faster in 1973, the final average leaf weight fell in between the 1971 and 1972 averages.

The average weight per leaf (total plant leaf weight per leaf number) was quite consistent among years. Average leaf weight was almost identical all three years at the time of the second harvest (0.30, 0.30, 0.33 gms, 1971, 1972 and 1973, respectively). This trend continued throughout the growing season and final average leaf weights were 0.52, 0.49 and 0.42 gms by years.

Increases in average total top dry weight for 5377, by definition, were similar with changes in amounts of leaf and stem dry weights.

Values for the average total plant leaf area changed in a fashion similar to the other measured variables in all three years. In 1971 plants grew in total leaf area almost twice as fast in the first half as in the second half of the season, whereas in 1972 mean total plant leaf area increased five times as fast in the first half of the year as in the second. However, while leaf area continued to increase in 1971 in the second half of the year, in 1972 it increased very little, primarily because leaf number showed little increase. Values for average total plant leaf area in 1973 were only about one-half the value of the 1972 trees at the second harvest time but final values were quite similar.

Average individual leaf area values for 1971 and 1972 increased constantly over the three harvests. Values for 1973 were consistent with the other two years at the second harvest but then decreased later in the season.

Clone 5339

Stem height growth of 5339 continued at a nearly constant rate throughout the growing season all three years, although rates were different in different years. There were also differences in final height attained. Trees grew the most in 1971, reaching a total height that was almost three times greater than that in 1972. Height growth in 1973 started slowly but by the final harvest the trees had increased in average height considerably, reaching a value midway between the 1971 and 1972 trees.

The trend in diameter growth was similar to that for height growth in 1971. Maximum values for diameter growth were found in 1971. Trees in 1972 showed very little increase in diameter during the first part of the season but then grew more rapidly. Values for 1972 mean stem diameter were less than one-half those found for trees in 1971 at both the second and third harvest times. Trees in 1973 also started out growing slowly but then increased at a rate faster than that for 1972 trees, so that final diameter values for clone 5339 in 1973 were between 1971 and 1972 values.

Large differences occurred between years both in rate of stem weight increase and in final dry weight accumulated. Trees in 1971 grew more percentage-wise in the first part of the season but continued to grow well in the second part of the year. Trees in 1972 started out extremely slowly and finished at final harvest time weighing one-eleventh as much as in 1971. Trees in 1973 started equally slowly but showed a large increase in stem weight later in the season. Differences also occurred in both leaf dry weight and leaf number between years. In 1971 trees grew best, making rapid growth in the first of the season then continuing to grow at a slower

rate for the remainder of the year. In 1972 growth was extremely slow, yielding relatively low values for both variables. Final leaf weight in 1972 was about one-tenth as much as for 1971 trees. In 1973 the growth of the trees was initially as slow as that in 1972 but increases in growth occurred later in the season. By the final harvest in 1973, leaf weight had increased 33 times over the low second harvest value of the same year.

Differences were apparent in average individual leaf weight. Although the trees grew at different rates in 1971 and 1973, final values were similar (0.43 gm in 1971, 0.34 gm in 1973); the final value for 1972 trees was 0.09 gm.

Increases in average total top dry weight for clone 5339, by definition, were indentical with changes in amounts of leaf and stem dry weights.

Rate and amount of leaf area production were similar to the performance of other variables. Final average total plant leaf area was greatest for 1971 trees and worst for 1972 trees; values for 1971 were about seven times greater than for 1972. Values for mean area of leaves from 1973 trees were only one-twentieth those for 1971 trees at the second harvest time but increased to a value close to that found in 1971 by the time of the third harvest. Changes in average individual leaf areas were similar to those for mean total plant leaf area changes.

Clonal comparisons between years at Ames

To compare clones across years, clones were ranked on the basis of their performance during each growing period for all three years. The results showed that 5377 ranked first for all variables measured for all three years and all harvest times. The pattern of growth for 5377 was

approximately the same in Ames for 1971 and 1972, with the height growth rate slowing somewhat in the second half of the growing season and other variables increasing during the same period. In 1973 all variables continued to increase throughout the entire growing season, with some variables showing greater increases in the last half of the growing season compared to the first half of the season.

The magnitude of the difference between the first ranked clone (5377) and the second ranked clone increased as the growing season progressed (Figure 1). There were also differences in rates of growth of each clone between years. This was reflected in the rankings of the three clones at the various harvest times. For example at harvest time one, the ranking was 5377, 5260, 5339 for all variables measured for both 1971 and 1972, except where 5260 approximately equaled 5339 in stem height in 1972. At harvest time two, the ranking was also 5377, 5260, 5339 for all variables measured for all three years, except where the ranking was 5377, 5339, 5260 for 1971 leaf area, weight and number. By harvest time three, however, the ranking was always 5377, 5339, 5260 for 1971 and 1973, whereas in 1972 the ranking for all variables was 5377, 5260, 5339. This change in ranking in 1972 was due to the poor growth of 5339 that year. Clone 5339 grew at a fairly constant rate throughout the season all three years, although there were large differences in the total amount of growth of the measured variables between years. For example the average total top dry weight of trees harvested at the end of the 1971 season was ten times heavier than those harvested at the end of the 1972 season.

Clone 5260 consistently set bud by the middle of the growing season all three years (Figure 2). Consequently, 5339 was often ranked in second

Figure 1. Mean total top dry weight (gms), by clone and harvest time, for first year growth at Ames in 1971. N = 3

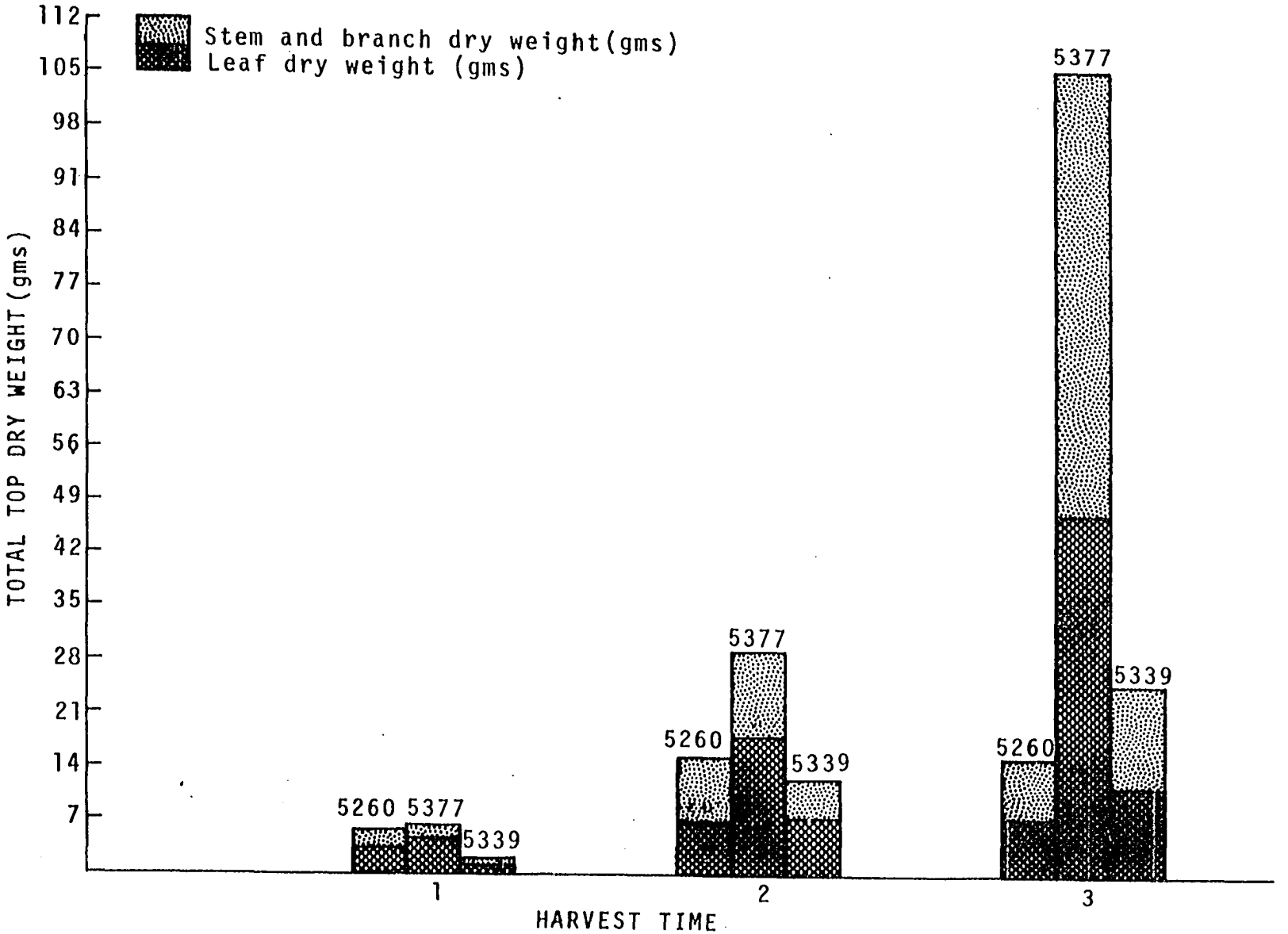
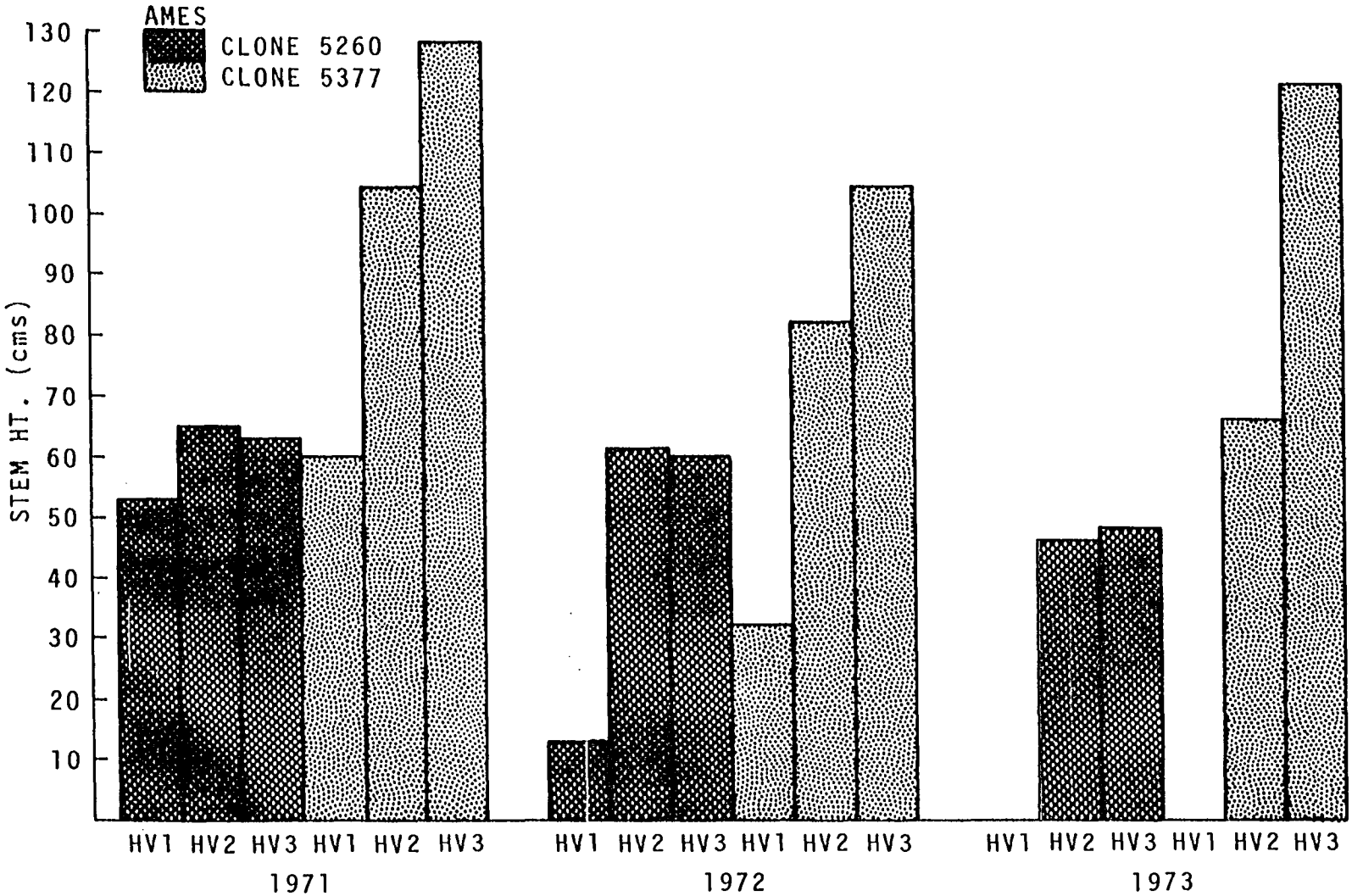

Stem and branch dry weight(gms)
Leaf dry weight (gms)
TOTAL TOP DRY WEIGHT(gms)
112
105
98
91
84
77
70
63
56
49
42
35
28
21
14
7
5260
5377
5339
5260
5377
5339
5260
5377
5339
1
2
3
HARVEST TIME

Figure 2. Mean stem height (cms), by year, clone and harvest, for first year growth at Ames. Hv = harvest time; N = 3


AMES
CLONE 5260
CLONE 5377
STEM HT. (cms)
130
120
110
100
90
80
70
60
50
40
30
20
10
HV1 HV2 HV3 HV1 HV2 HV3
1971
HV1 HV2 HV3 HV1 HV2 HV3
1972
HV1 HV2 HV3 HV1 HV2 HV3
1973

place by the end of each season because it continued to grow throughout the entire season.

The relative composition of the total top dry weight did not vary much either among clones within years or among years. Stem weights as a percentage of total top dry weight for third harvest trees, when averaged over three years, including all clones was 49.2%. Individual clonal averages were 46% for 5260, 49.7% for 5377 and 52% for 5339.

Field Growth: Harvest Data, by Clones, for Rhinelander First Year Growth

Clone 5260

Stem growth was limited in 1971 because all clones were not planted until July 12th that year (Table 5). By the time of the first harvest in 1971, all trees had set bud; the mean increase in stem height for the third harvest was probably due to sample variation. In 1972, 5260 grew faster than either of the other two clones until shortly after the time of the second harvest when height growth slowed markedly; height growth was significantly better in 1972 compared to the other growing seasons (Table 6). In 1973 trees again grew in height until the second harvest date when the rate of growth slowed markedly (Table 7).

Stem diameter growth in 1971 again reflected the fact that it had been planted late in the season. However, values for the first harvest in 1971 were greater than first harvest values measured in other years although all clones in Rhinelander in 1971 developed under a longer photoperiod, as compared to other years, by virtue of the late planting date. Diameter growth patterns for 1972 and 1973 were similar and final diameter values

Table 5. Means by variable, clone and harvest for the 1971 growing season at Rhinelander

Harvest	Clone	Dependent variables SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW (gm)	LA_2 (cm^2)	LF
1[a]	5260	No trees harvested						
	5377	No trees harvested						
	5339	No trees harvested						
2[a]	5260	26.7	0.243	1.68	1.19	2.87	195.3	17.3
	5377	36.7	0.230	1.87	0.81	2.68	273.0	25.7
	5339	40.4	0.230	2.74	1.18	3.92	322.3	17.7
3[ab]	5260	28.2	0.276	3.19	1.74	4.93	220.0	15.0
	5377	79.2	0.412	12.68	8.72	21.40	1509.3	37.0
	5339	79.8	0.435	11.59	7.20	18.79	1147.7	23.0

[a]N = 3 for all harvests.

[b]Harvest 3 made at end of two-month growing period.

Table 6. Means by variable, clone and harvest for the 1972 growing season at Rhinelander

Harvest	Clone	Dependent variables SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW (gm)	LA_2 (cm^2)	LF
1[a]	5260	14.0	0.186	1.36	0.50	1.86	194.7	11.3
	5377	21.7	0.247	1.59	0.43	2.02	246.3	13.7
	5339	9.4	0.106	0.17	0.11	0.28	27.3	6.7
2[a]	5260	60.3	0.363	4.87	3.75	8.62	969.3	24.7
	5377	53.4	0.366	8.99	2.70	11.69	1379.0	49.0
	5339	26.2	0.211	1.25	0.56	1.81	217.0	18.7
3[a]	5260	72.5	0.374	18.94	11.81	30.83	1288.7	27.7
	5377	124.2	0.633	46.50	31.23	77.73	4730.7	64.0
	5339	29.2	0.182	3.01	1.31	4.32	312.5	9.5

[a]N = 3 for all harvests.

Table 7. Means by variable, clone and harvest for the 1973 growing season at Rhinelander

Harvest	Clone	Dependent variables SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW (gm)	LA_2 (cm^2)	LF
1[a]	5260	22.7	0.226	1.22	0.67	1.89	158.0	14.0
	5377	24.0	0.230	1.26	0.43	1.69	227.7	17.7
	5339	23.7	0.189	0.77	0.30	1.07	129.3	16.3
2[a]	5260	46.7	0.326	6.92	3.35	10.87	848.0	46.0
	5377	61.3	0.308	5.95	3.17	9.12	889.0	26.0
	5339	50.3	0.251	3.32	1.73	5.08	660.0	19.0
3[b]	5260	55.2	0.355	5.83	5.59	11.42	669.7	22.5
	5377	91.1	0.448	13.00	11.57	24.57	2195.7	30.2
	5339	80.8	0.383	9.26	7.28	16.72	1488.0	27.4

[a] N for harvests 1 and 2 = 3.

[b] N for harvest 3 = 9.

were approximately equal. In all three years, diameter growth slowed considerably with the cessation of height growth.

Stem dry weights showed greater "one-month" growth in 1971 than other years, although the growing period was not seasonally the same. Following bud set, stem dry weights in 1971 showed little gain.

Rate of stem dry weight increase was about the same in 1972 and 1973 until the time of the second harvest. However, following this period stem dry weight in 1972 increased more than three times, while in 1973 it increased about 67% as compared to a 19% height increase for both years. Final stem dry weights for 1972 were more than two times the 1973 average value. However, clonal differences and the harvest x clone interaction in

1971 were not significant at the .05 level due to high variability in the measurements (Table 8).

Following bud set in 1971, leaf weight increased but leaf number decreased slightly, possibly due to sample variation. Growth in leaf weight was similar for the first month in 1972 and 1973. However, differences did occur in both leaf weight and leaf number following that period, with trees in 1973 showing greater values for both. By the end of the season in 1972, however, leaf weight had increased approximately four times over the value at the second harvest time, whereas the weight in 1973 showed no gain. Accompanying these changes in leaf weight was the fact that leaf number increased only slightly in 1972 and showed no increase in 1973.

In 1971, 5260 showed more "first month" top dry weight because it had been planted later in the season than trees in 1972 and 1973. Trees in 1971 gained in total top dry weight after bud set largely because of increased leaf weight.

Trees in 1972 increased greatly in total top weight after the second harvest date because of increases in both leaf and stem dry weight. Final total top weight values in 1972 were almost three times those found in 1973. Due to the high variability of measurements, clonal differences in total top dry weight were not significant at the .05 level in either 1971 or 1973 (Table 8).

Average total plant leaf area increased only slightly for those trees planted in 1971; clonal differences were nonsignificant. In 1972 and 1973 average total plant leaf area increased approximately the same amount until the time of the second harvest. Following that time, however, plants in

Table 8. Mean square values by variable and year for first year harvest data at Rhinelander

Source and year	DF	Dependent variables: SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW (gm)	LA_2 (cm^2)	LN
1971		<.01	<.01	<.01	<.01	<.01	.02	.08
Harvest	1	539.01	0.09	224.20	104.95	636.21	2176393.39	102.72
		<.01	.05	.06	.15	.09	.12	<.01
Clone	2	309.38	0.01	45.74	18.68	122.33	769640.70	368.39
		.04	.03	.09	.12	.10	.18	.12
Harvest x clone	2	120.15	0.01	36.06	21.92	114.21	569531.05	70.39
Error	6	22.09	0.002	9.83	7.14	32.70	245501.60	22.94
1972		<.01	<.01	<.01	<.01	<.01	<.01	<.01
Harvest	2	7134.54	0.10	1113.84	459.57	3343.91	8649514.00	1310.74
		<.01	<.01	<.01	<.01	<.01	<.01	<.01
Clone	2	3988.00	0.12	571.01	234.36	1905.29	7113336.50	2060.03
		<.01	.02	<.01	<.01	<.01	<.01	.06
Harvest x clone	4	1425.61	0.02	297.54	185.00	997.53	3455370.70	421.98
Error	7	92.33	0.004	3.99	2.06	15.08	84373.00	
1973		<.01	<.01	<.01	<.01	<.01		<.01
Harvest	2	9582.34	0.12	244.23	242.82	976.08	--	531.23
		<.01	.01	.08	.10	.09		<.04
Clone	2	873.69	0.01	18.59	14.00	62.50	--	126.37
		.02	.02	.01	.03	.01		<.01
Harvest x clone	4	440.23	0.01	29.78	17.73	97.25	--	346.36
Error	28	121.59	0.001	6.60	5.52	23.48	--	36.18

1972, while gaining only slightly in leaf number, gained one-third in leaf area, while those in 1973 showed an area decrease due to a decrease in leaf number in the sample trees.

By examining average individual leaf area, it can be seen that the average leaf size did increase for both 1972 and 1973 throughout the growing season.

Clone 5377

Height growth of 5377 was variable in different years, although trends were somewhat consistent over the three growing seasons.

In 1971, 5377, unlike 5260, grew steadily in the last one-half of the growing season. Growth for the two months the clone was in the field in 1971 surpassed the first two month's growth for trees planted in both 1972 or 1973, although the times were not seasonally comparable.

Trees grew in height at about the same rate in 1972 and 1973 through the second harvest. Growth after this time, however, increased greatly in 1972 whereas in 1973 height made smaller but significant increases.

Trees increased proportionately the same in diameter growth and height growth in the second half of the growing season in 1973, whereas in 1971 and 1972 growth in height was proportionately larger. Measurement of the diameter of the trees grown in 1973 produced widely varying values, as opposed to the 1972 season where there was more consistency in growth between sample trees.

Stem weights varied among the three growing seasons both in rate of growth and in total accumulation of photosynthate. Trees planted late in 1971 had the best growth rate (weight per time) of any of the other two-

month periods; by the second harvest time, the average stem weight had increased to 11 times the first harvest value. Trees in 1972 and 1973 grew similarly in stem weight up to the second harvest time. However, the 1972 trees then proceeded to far outgrow those planted in 1973. Growth in stem weight in both 1971 and 1972 was similar to growth in other variables.

Growth for both leaf weight and number was similar to the previously discussed growth performance for other variables. Late-planted 1971 trees grew best in this two-month period in leaf weight compared to the first two-month growth of earlier planted 1972 and 1973 trees.

Again growth for 1972 and 1973 was similar up until the date of the second harvest for all variables except leaf weight, number and area, which were larger in 1972. Following this date, trees planted in 1972 grew much more rapidly than trees in 1973. Final harvest data showed that the average total plant leaf weight of 1972 planted trees was almost four times greater than that of trees planted in 1973; final leaf number was more than twice as large. The average individual leaf weight increased throughout the season for all three years.

Rate and amount of the average total top dry weight growth was similar by definition to leaf and stem weight growth patterns. Growth of trees planted in 1972 was similar to growth in 1973 up until the second harvest date. The most rapid gains were made in the last half of the growing season in 1972. In all instances, the leaf weight contributed the highest percentage to the final total top dry weight. The amount of leaf weight contributing to the total top dry weight, however, decreased throughout the growing season. Final harvest data for 1972 for 5377 trees showed that

total top dry weight was 60% leaf and 40% stem weight; 1973 trees were composed of 53% leaf and 47% stem weight.

Gains in the average total plant leaf area were similar to the growth performance of the other variables. Final average total plant leaf areas for 1972 plants were more than twice those for 1973 plants; however, the final average individual leaf area was similar for both 1972 and 1973 plants (approximately 74 cm).

Clone 5339

Height growth of 5339 varied greatly among the three different years. Trees planted in 1972 exhibited poor growth compared with 1971 and 1973 trees; growth was slow in starting in the first half of the season and there was little growth in the last half of the season. Trees planted in 1971, on the other hand, grew well for the two late season months they were in the field; trees in 1973 also grew well throughout the growing season.

Growth in diameter was similar in seasonal pattern to height growth. Trees in 1972 grew much less than those planted in 1971 or 1973. Trees planted late in the season in 1971 grew more in diameter in the two months they were at the site than trees of either of the other two years that were at the site three months. Final harvest diameters for the 1973 trees were more than twice of those planted in 1972.

The gain in stem dry weights further showed large yearly differences for clone 5339. Stem weights for the two-month 1971 season were equal to those for the three-month 1973 season.

The trend for leaf weight growth was the same as for several previously discussed variables: 1971 growth surpassed full season growth of the other two seasons, and in 1972, 5339 grew quite slowly.

Leaf number was maximum at mid-season in 1972, while plants in 1973 initiated leaves throughout the growing season. The weights of the average leaf for the final harvest in 1972 and 1973 were approximately equal (.32 and .34 gms, respectively).

The total top dry weight growth was again greatest for the two-month 1971 plants and least for the 1972 plants. Leaf material was always more than half of the average total top dry weight. This proportion was maintained quite uniformly throughout the growing season.

The average total plant leaf area varied considerably both within and between the three growing seasons. The leaf area of the 1972 plants was far below both the 1971 plants (two-month growing period) and the 1973 plants (three-month growing period). Plants in 1973 continued to expand their leaves throughout the growing season although a small sample size prevented a test of significance.

The average individual leaf area also differed in different years: the value for the 1972 trees was lowest (33 cm^2), while the value for the two-month 1971 plants was approximately equal to the 1973 three-month value (50 and 54 cm^2, respectively).

Clonal comparisons between years at Rhinelander

In order to compare clonal performance among years, clones were ranked on the basis of their performance during each growing period for all three years. The results showed that 5377 ranked first for the majority of vari-

ables measured for all three years for all harvests, although differences in ranking did occur at various harvest times in different years. In 1971 and 1973, 5330 and 5260 usually ranked second and third, respectively, while in 1972 the rankings were reversed (Figure 3).

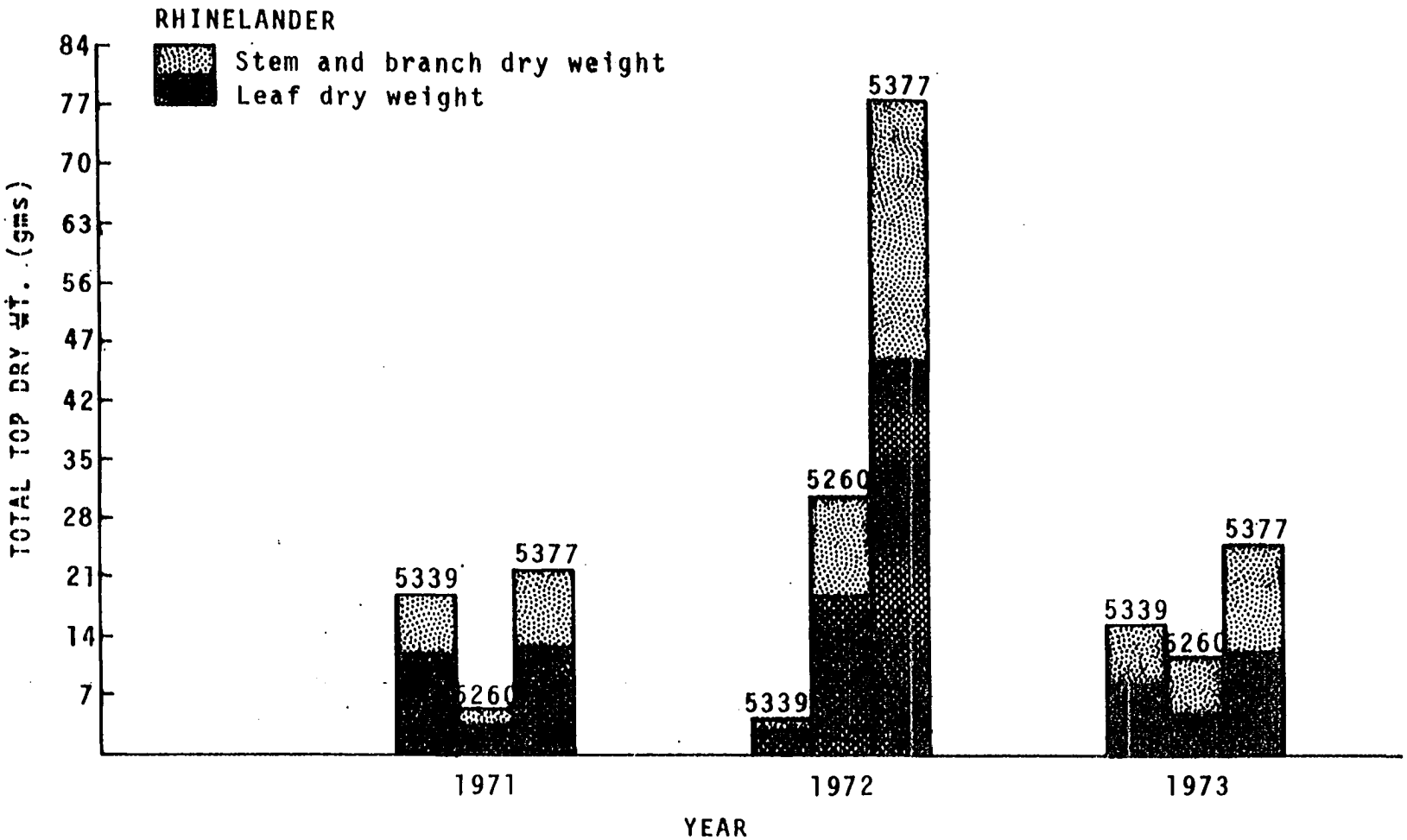
In general 5260 grew in the same fashion in both 1972 and 1973; increases in all the variables measured occurred through the first half of August when growth ceased or slowed markedly. However, there were large differences in accumulation of photosynthate between the two years; plants in 1972 were considerably larger in all categories except stem diameter and leaf number. In 1971, 5260 was planted too late in the season for significant growth increases.

Growth of 5377 differed in the years 1972 and 1973 although final rankings showed it to be the top ranked clone for both years. In 1972 the rate of height and diameter growth of clones 5377 and 5260 was approximately the same throughout the first one-half of the growing season although there were large differences in leaf characteristics (weight, area, leaf number); in 1973 the growth of 5377 lagged behind the growth of 5260 for many variables through the first one-half of the growing season but far surpassed 5260 by the end of the year. In 1971 clone 5377 grew steadily throughout the last one-half of the year.

The growth of 5339 was extremely poor in 1972 for all variables measured (Figure 3). In 1973, however, 5339 grew nearly as well as clone 5377 in height, diameter and leaf number although final stem weight of 5377 was 58% greater than that of 5339. Growth of 5339 in 1971 was similar to 5377.

Stem weight as a percentage of the total top dry weight for third harvest trees, when averaged over two years (1972, 1973), including all

Figure 3. Mean total top dry weight (gms), by year and clone, for the third harvest data for first year growth at Rhinelander. 1971 growth data based on two-month growing period. N = 3


RHINELANDER
Stem and branch dry weight
Leaf dry weight
TOTAL TOP DRY WT. (gms)
84
77
70
63
56
47
42
35
28
21
14
7
5339
5260
5377
5339
5260
5377
5339
5260
5377
1971
1972
1973
YEAR

clones, was 41%. Individual clonal averages were 43.5% for 5260, 43.5% for 5377 and 37% for 5339. Large variability in the rate of growth of all clones caused many comparisons to be nonsignificant in Rhinelander in 1971. Growth variances were less in 1973 and relatively small in 1972.

Clonal Comparisons of Harvest Data between Locations

Clone 5260, in Ames, consistently set bud by the first part of August, whereas in Rhinelander it grew slightly longer. In Ames the clone showed about the same trends all three years but in Rhinelander it grew differently in different years. For example at the end of the 1972 growing season, the total top dry weight of the clone at Rhinelander was almost twice that in Ames, while in 1973 the weights were almost identical. Final measurements showed that growth of clone 5260 for all variables was similar for the years 1971, 1972 and 1973 in Ames and 1973 in Rhinelander; growth in 1972 in Rhinelander far exceeded all these years for many variables and growth in 1971 was not strictly comparable due to late planting. Rankings of final harvest material showed 5260 to be in last place for all variables measured at both locations in 1971 and 1973 and in second place in 1972 for all variables.

In Ames 5377 always ranked ahead of 5339 and 5260 at all harvest times for all three years. In Rhinelander, changes in rank occurred at the various harvest times within years but clone 5377 did rank ahead of the other two clones most of the time. However, the magnitude of the difference between the first and second ranked clones was not as consistently large as in Ames. In 1972, 5377 grew better with respect to six variables at Rhinelander; only stem diameter was slightly larger in Ames. Largest dif-

ferences occurred in the variables leaf weight, area and number, all being much larger at Rhinelander. In 1973, 5377 grew better with respect to all seven variables at Ames. Stems at Ames weighed more than three times as much as at Rhinelander and were 34% taller. Smallest differences occurred in leaf area, even though the average leaf number was 145% greater and the average leaf weight was 139% greater in Ames. Growth patterns for clone 5377 were similar at both locations.

Clone 5339 grew throughout the growing season at both locations for all three years, although it did not grow well at either location in 1972. In Ames initial growth of 5339 was generally the slowest of the three clones but by the end of the growing season (1971, 1973) it had surpassed 5260 due to the latter's habit of early bud set. Thus, the ranking for the final harvest material for these two years in Ames was 5377, 5339 and 5260. This was similar to the growth behavior of 5339 in Rhinelander in 1973 where the final rankings were also 5377, 5339 and 5260. In Rhinelander in 1971, when trees were planted a month later than normal, initial growth of 5339 exceed that of 5377 and 5260. In 1972, 5339 grew best in Ames with respect to stem height, stem diameter and leaf number and in Rhinelander in leaf weight, total top dry weight and leaf area; stem weights were nearly identical. In 1973 growth of 5339 was clearly best in Rhinelander for stem height, stem diameter and leaf area; other variables had similar values with leaf weight and stem weight being only slightly larger in Ames.

Differences existed between locations with respect to the partitioning of photosynthate into leaves and stems within clones. The overall percentage of stem wood in the total top dry weight was 8% lower in Rhinelander than in Ames, when averaged for all clones over two and three years,

respectively, for third harvest material (41.0% in Rhinelander versus 49.2% in Ames). In examining the individual clonal behavior, it was found that little difference existed between locations in amount of photosynthate partitioned into stem wood for 5260 (46% in Ames versus 44% in Rhinelander); differences were slightly larger for the 5377 (50% in Ames, 44% in Rhinelander) and fairly large differences existed for 5339 (52% in Ames and 37% in Rhinelander).

In summary, then, 5377 ranked in first place at both the Ames and Rhinelander sites by the end of each respective growing season for all three years for all variables. Clone 5339 ranked in second place at both locations for almost all variables measured by the end of both the 1971 and 1973 seasons; poor growth of 5339 in 1972 resulted in its ranking third in 1972. Clone 5260 ranked in last place for all variables measured at both locations for the years 1971 and 1973; although 5260 did not grow noticeably better in 1972, except in Rhinelander, it ended ranked second by virtue of poor growth of 5339 in 1972.

In general growth trends were the same at both locations for the years 1971 and 1973; 1972 growth differed from those two years but differed in the same fashion at both locations.

Field second- and third-year-old growth: Ames and Rhinelander

Trees that were not harvested by the end of the 1971 and 1972 growing seasons were left at the site to obtain information about two- and three-year-old material. Again rankings by size were used to compare clones (Table 9). Rankings for two-year-old trees in Ames (planted 1972, harvested 1973) were 5377, 5339 and 5260 for the variables stem height and

Table 9. Means by variable, clone, year and location for second and third year growth

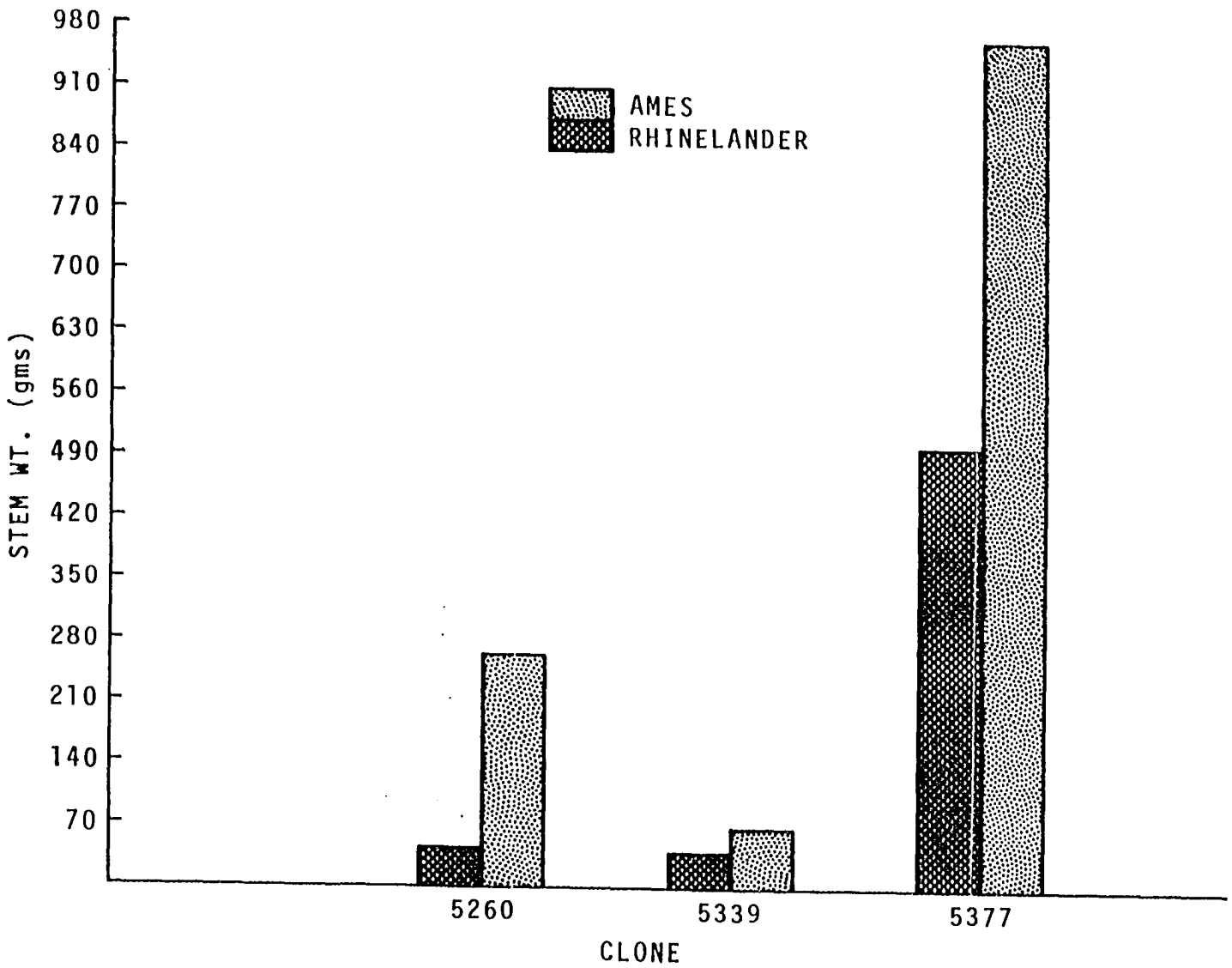
Location	Year planted[a]	Clone	Dependent variables SH (cm)	SD (in)	SW (gm)	LW (gm)	TTW (gm)	LN
Ames	1971	5260	203.7	1.31	281.6	--	--	--
		5377	327.3	2.19	1019.0	--	--	--
		5339	431.8	2.98	2286.8	--	--	--
	1972	5260	85.5	0.58	46.3	--	--	--
		5377	295.8	1.69	505.7	--	--	--
		5339	114.3	0.62	44.1	--	--	--
Rhinelander	1971	5260	203.9	1.06	202.1	--	--	--
		5377	387.0	2.08	1136.7	--	--	--
		5339	327.8	1.81	815.7	--	--	--
	1972	5260	176.8	1.23	274.1	145.6	419.7	382.0
		5377	287.2	2.33	963.6	601.6	1565.2	1211.2
		5339	135.0	0.72	69.8	72.9	142.7	191.0

[a]All trees harvested at end of 1973 growing season. N varies from 3 to 8.

stem diameter; stem weight ranking was 5377, 5260 and 5339. For Rhinelander two-year-old trees, the ranking was 5377, 5260 and 5339 for the same variables. However, all three clones were larger in Rhinelander than in Ames after two years with respect to stem diameter and stem dry weight. For example, stem weight of 5260 at Rhinelander was six times that in Ames; stem weight of 5377 was more than two times the Ames weight, even though there was only a 3% difference in height (Figure 4).

Three-year-old rankings (planted 1971, harvested 1973) for the Ames trees were 5339, 5377 and 5260 for all three variables measured. At Rhinelander, the ranking was 5377, 5339 and 5260. In general after three years

Figure 4. Mean stem dry weight (gms), by location and clone, for two-year-old trees (planted 1972, harvested 1973)


980
910
840
770
700
630
560
490
420
350
280
210
140
70
STEM WT. (gms)
AMES
RHINELANDER
5260
5339
5377
CLONE

in the field, 5339 grew much better at Ames, 5377 grew only slightly better at Rhinelander and growth of 5260 was similar at both locations. Mean square values for second and third year growth harvest data are shown in Table 10.

Field Growth: Bi-monthly Measurements of Height and Leaf Number, One-Year-Old Material

Ames

Although there were differences between years at Ames, height growth of 5260 generally ceased by the end of July or the first part of August at Ames (Figure 5). Similarly, leaf production by these trees also generally ceased by the middle to end of July for all three years (Figure 8).

Height growth of the 5377 at Ames continued throughout almost the total growing season, although the rate of height growth slowed at about the same time each year at the end of August (Figure 6). Little variation was evident in either the rate of growth or in the final measurement values between years. Larger variances were found in relation to the rate and final amount of leaf production between years (Figure 9). In 1973, for example, although final stem heights were approximately equal to that of other years for 5377, leaf number was considerably below the values found in 1971 and 1972. Perhaps this was due to a larger number of leaves on branches in 1971 and 1972.

Clone 5339 at Ames showed wide variation in both the rate of increase and the final values of stem height and leaf number between years, although trends were similar (Figures 7 and 10).

Ranking of clones based on the final measurement of bi-monthly data agreed with ranking based on harvest data: in 1971 and 1973 the ranking

Table 10. Mean square values for clone by variable, years and location for second and third year harvest data

Location	Year planted[a]	Source	DF	Dependent variables SH (cm)	SD (in)	SW (gm)	LW (gm)	TTW (gm)	LN
				<.01	<.01	<.01			
Ames	1971	Clone	2	54569.10	2.67	3606666.50	--	--	--
		Error	7	743.73	0.14	236131.70	--	--	--
				<.01	<.01	<.01			
Rhinelander	1971	Clone	2	54380.20	1.75	1319384.00	--	--	--
		Error	14	1318.59	0.12	100794.63	--	--	--
				<.01	<.01	<.01			
Ames	1972	Clone	2	48933.60	2.18	38287.93	--	--	--
		Error	8	247.40	0.02	8245.12	--	--	--
				<.01	<.01	<.01	<.01	<.01	<.01
Rhinelander	1972	Clone	2	32232.20	3.03	1186968.50	456001.95	3076924.80	1604366.90
		Error	10	527.63	0.07	14689.14	2928.14	26944.83	14689.10

[a]All trees harvested at end of 1973 growing season.

Figure 5. Mean stem height (cms) of clone 5260, by year and measurement time, at Ames. N = 9

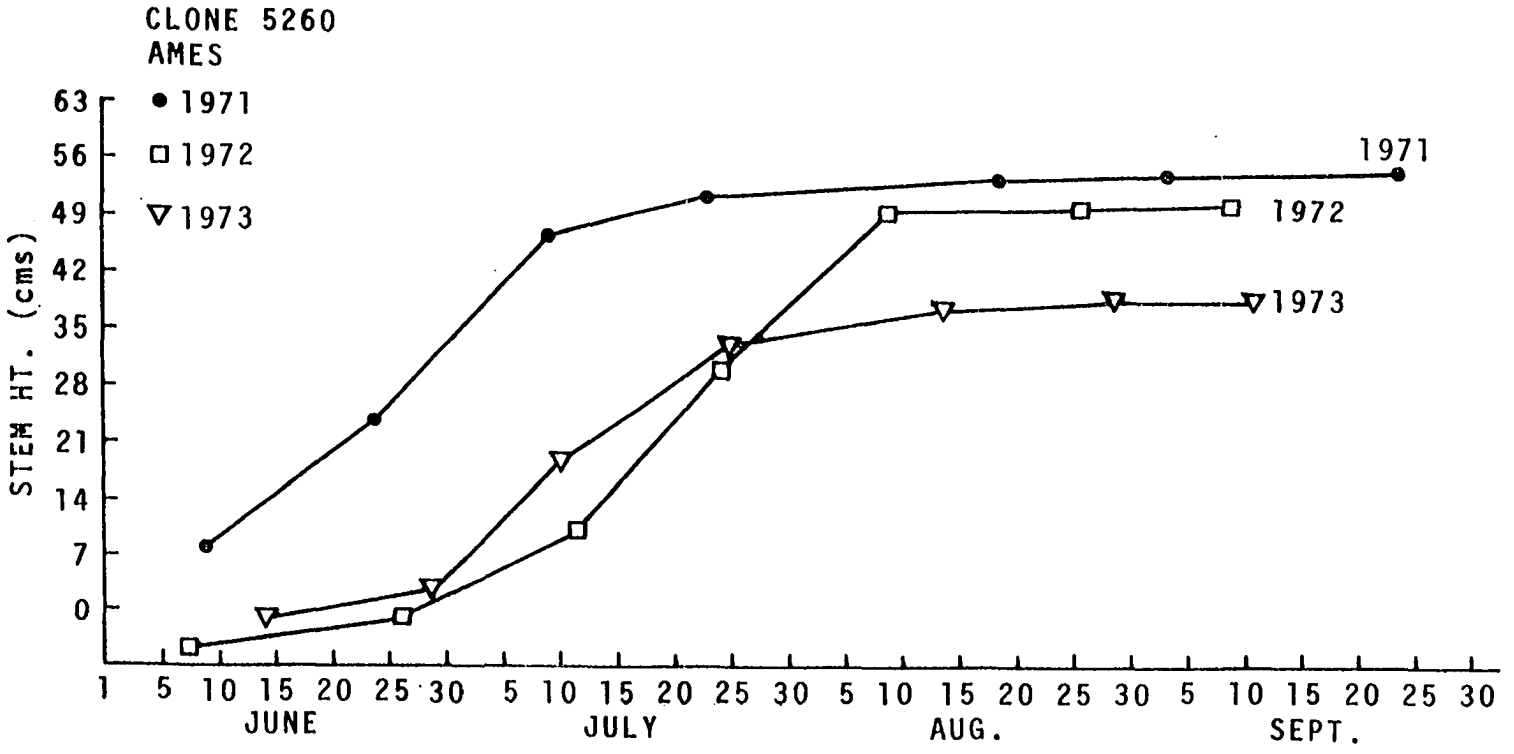

CLONE 5260
AMES
● 1971
□ 1972
▽ 1973
STEM HT. (cms)
63
56
49
42
35
28
21
14
7
0
1971
1972
1973
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 6. Mean stem height (cms) of clone 5377, by year and measurement time, at Ames. N = 9

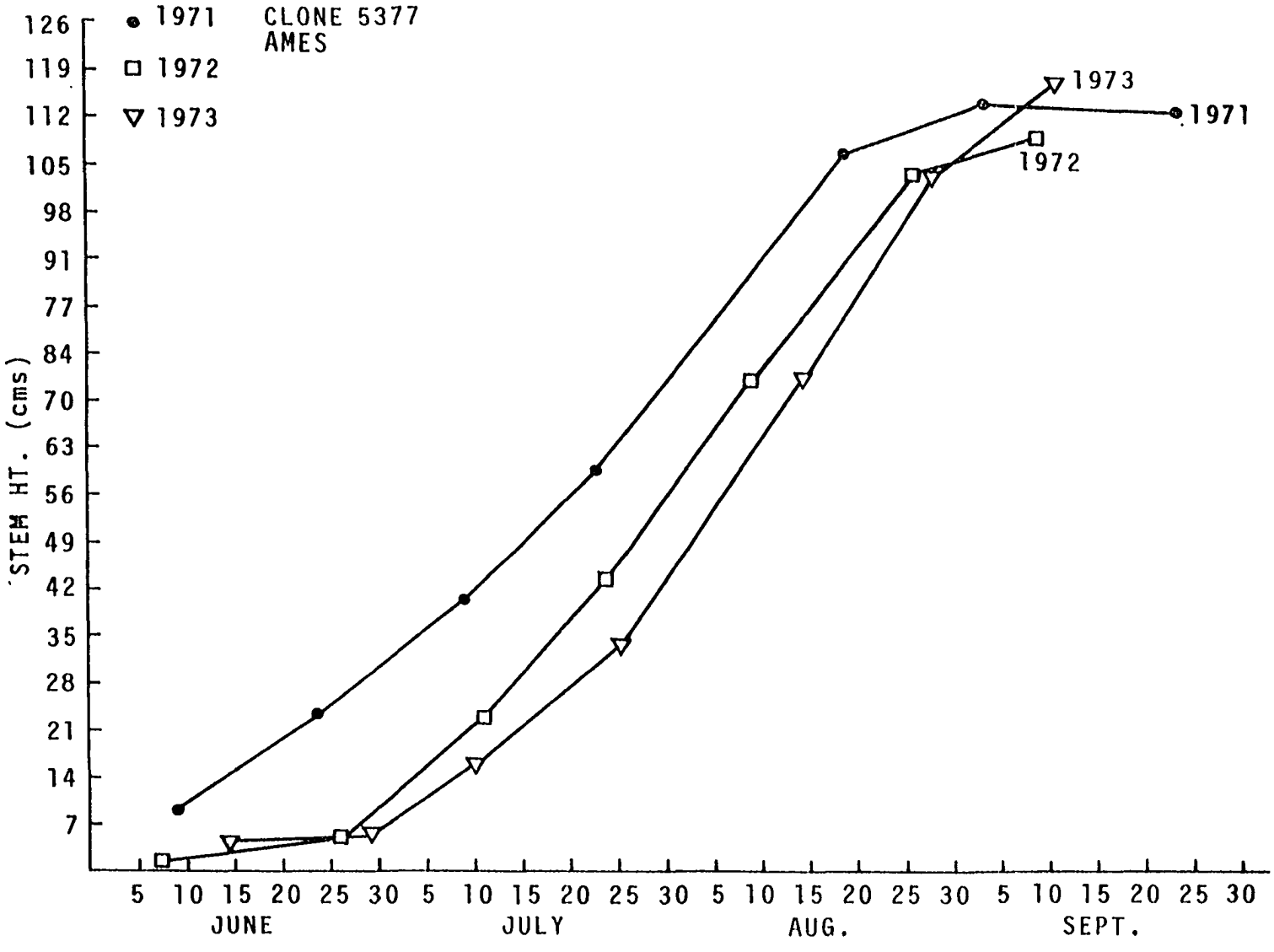

1971
1972
1973
CLONE 5377
AMES
126
119
112
105
98
91
77
84
70
63
56
49
42
35
28
21
14
7
STEM HT. (cms)
1973
1971
1972
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 7. Mean stem height (cms) of clone 5339, by year and measurement time, at Ames. N = 9

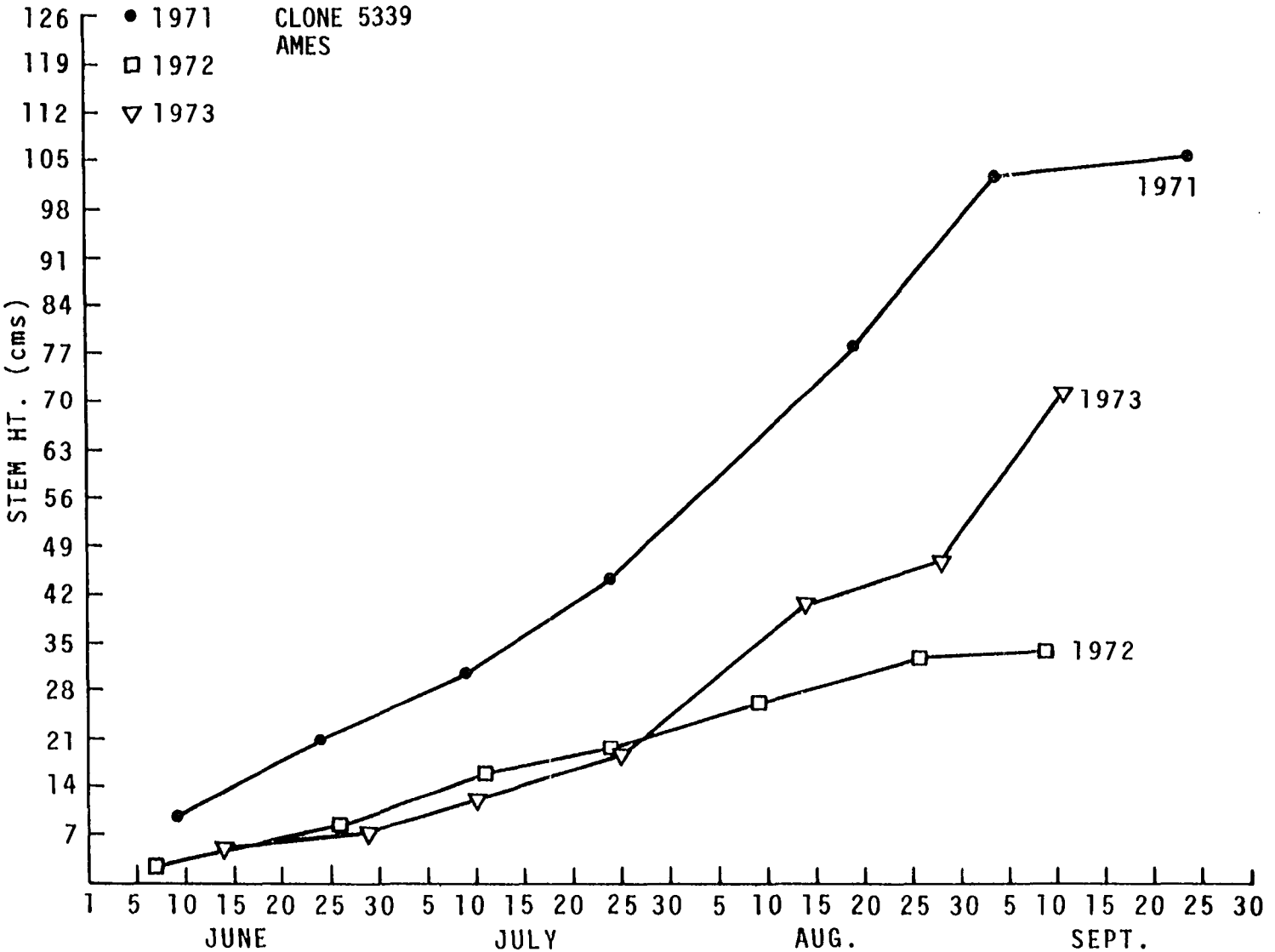

CLONE 5339
AMES
1971
1972
1973
STEM HT. (cms)
126
119
112
105
98
91
84
77
70
63
56
49
42
35
28
21
14
7
1971
1973
1972
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 8. Mean leaf number of clone 5260, by year and measurement time, at Ames. N = 9

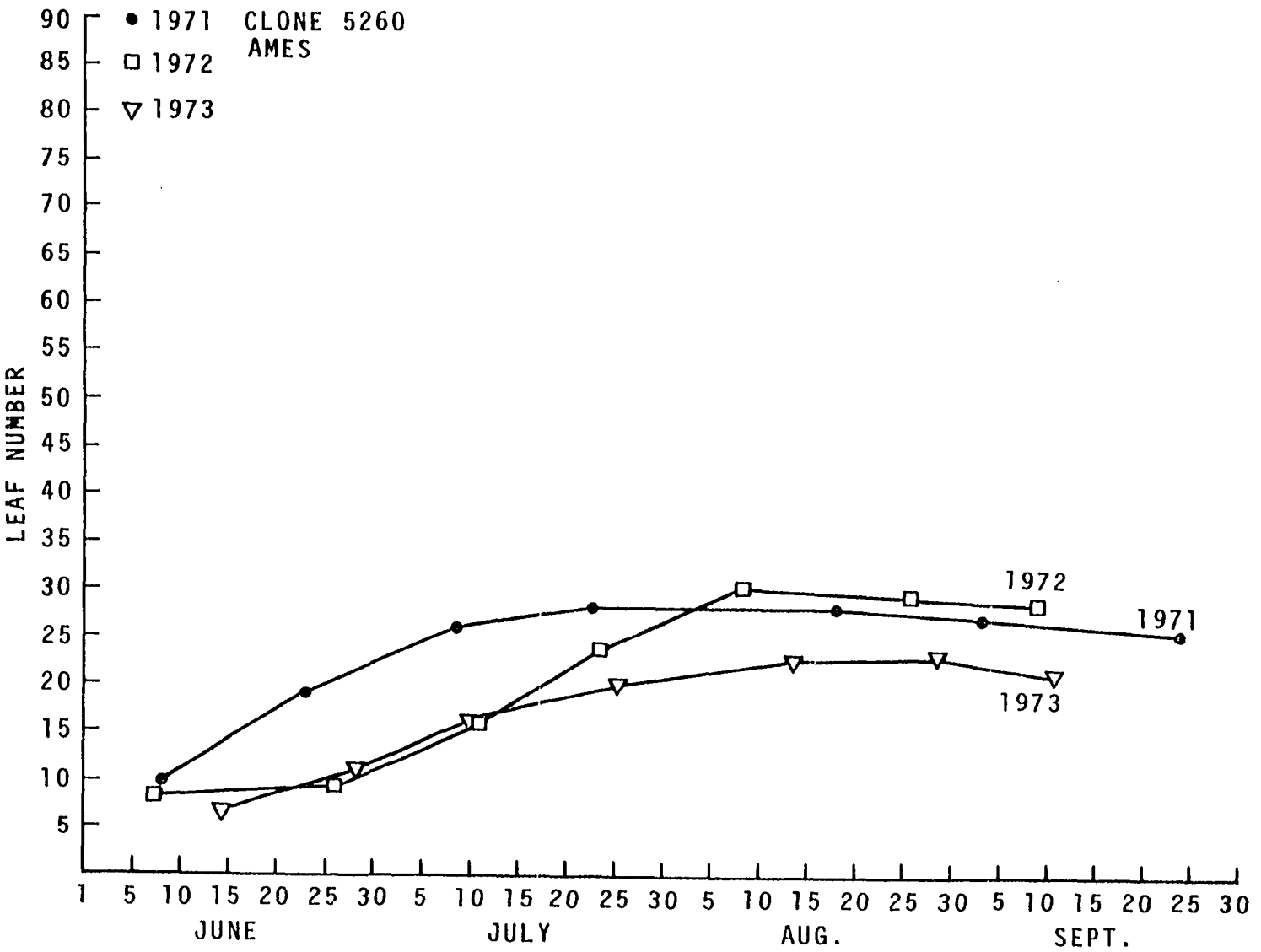

• 1971 CLONE 5260
AMES
□ 1972
▽ 1973
LEAF NUMBER
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
1972
1971
1973
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 9. Mean leaf number of clone 5377, by year and measurement time, at Ames. N = 9

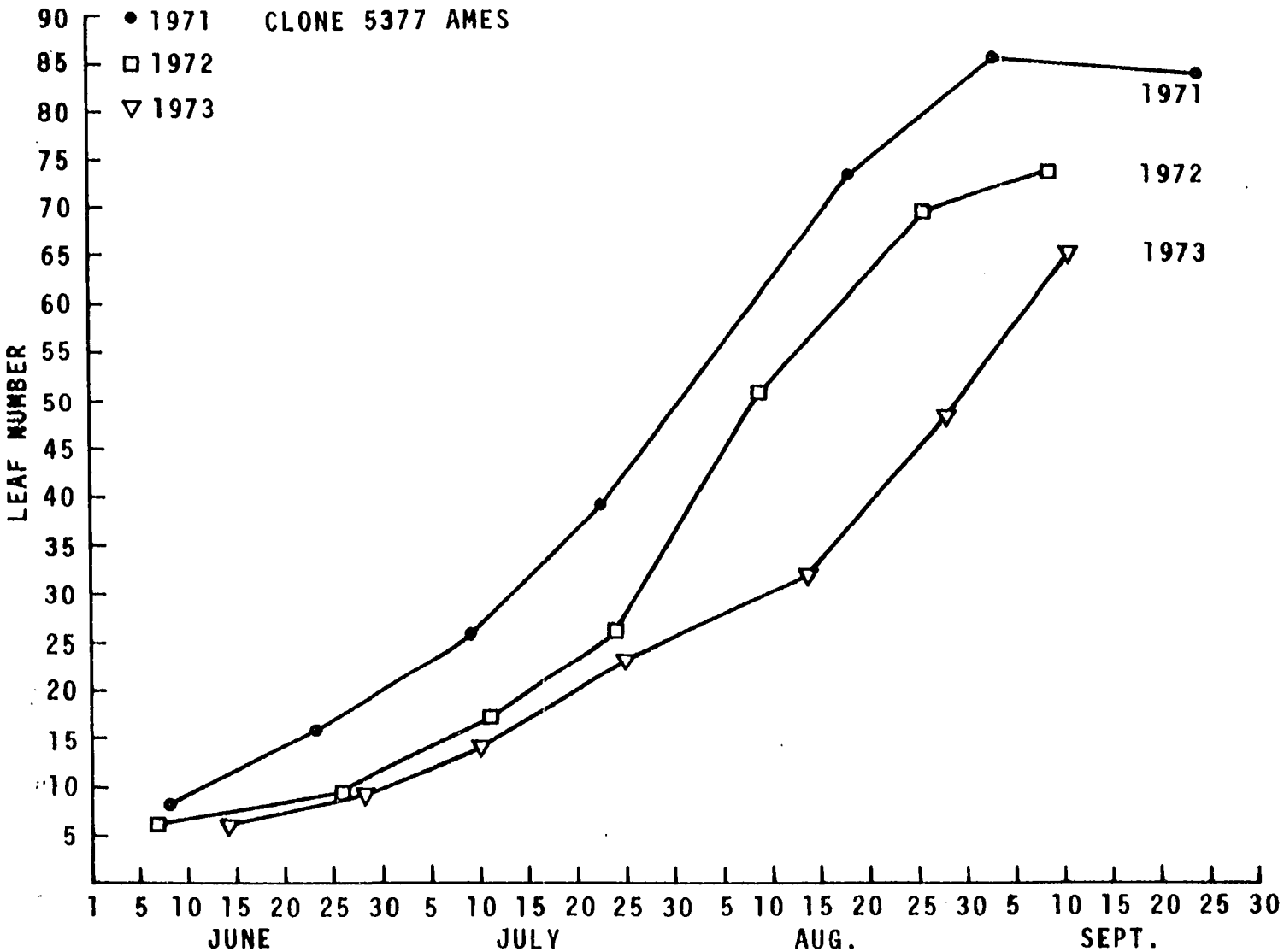
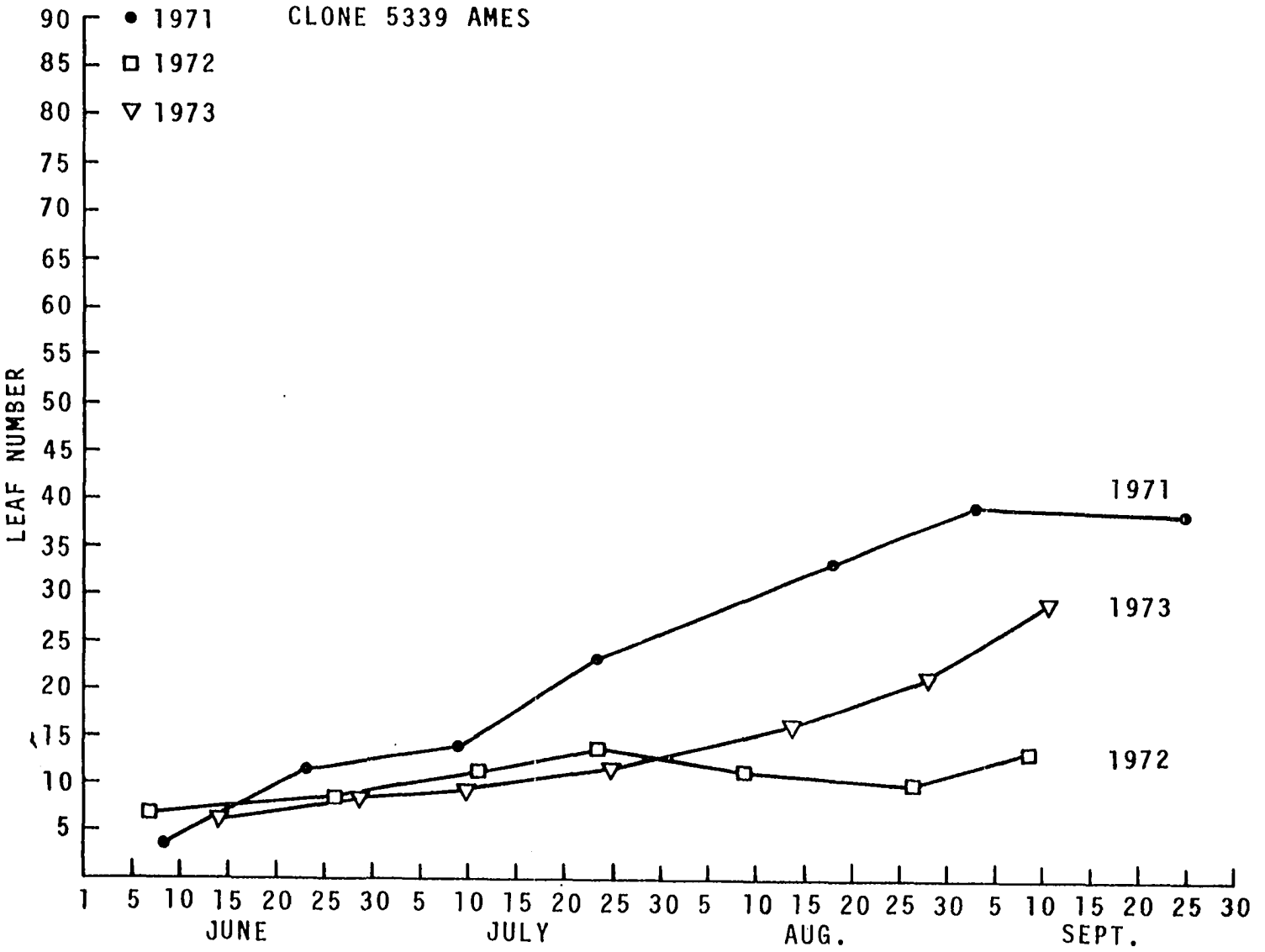

• 1971
□ 1972
▽ 1973
CLONE 5377 AMES
LEAF NUMBER
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
1971
1972
1973
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 10. Mean leaf number of clone 5339, by year and measurement time, at Ames. N = 9


CLONE 5339 AMES
1971
1972
1973
LEAF NUMBER
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
1971
1973
1972
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

was 5377, 5339 and 5260 and in 1972 it was 5377, 5260 and 5339 for both variables measured. Rankings for 1972 were unlike those for the other two years due to the poor growth of 5339 in 1972. Mean square values for first year bi-monthly measurements at Ames are shown in Table 11.

Table 11. Mean squares and F-values by variable and year for first year bi-monthly measurements at Ames

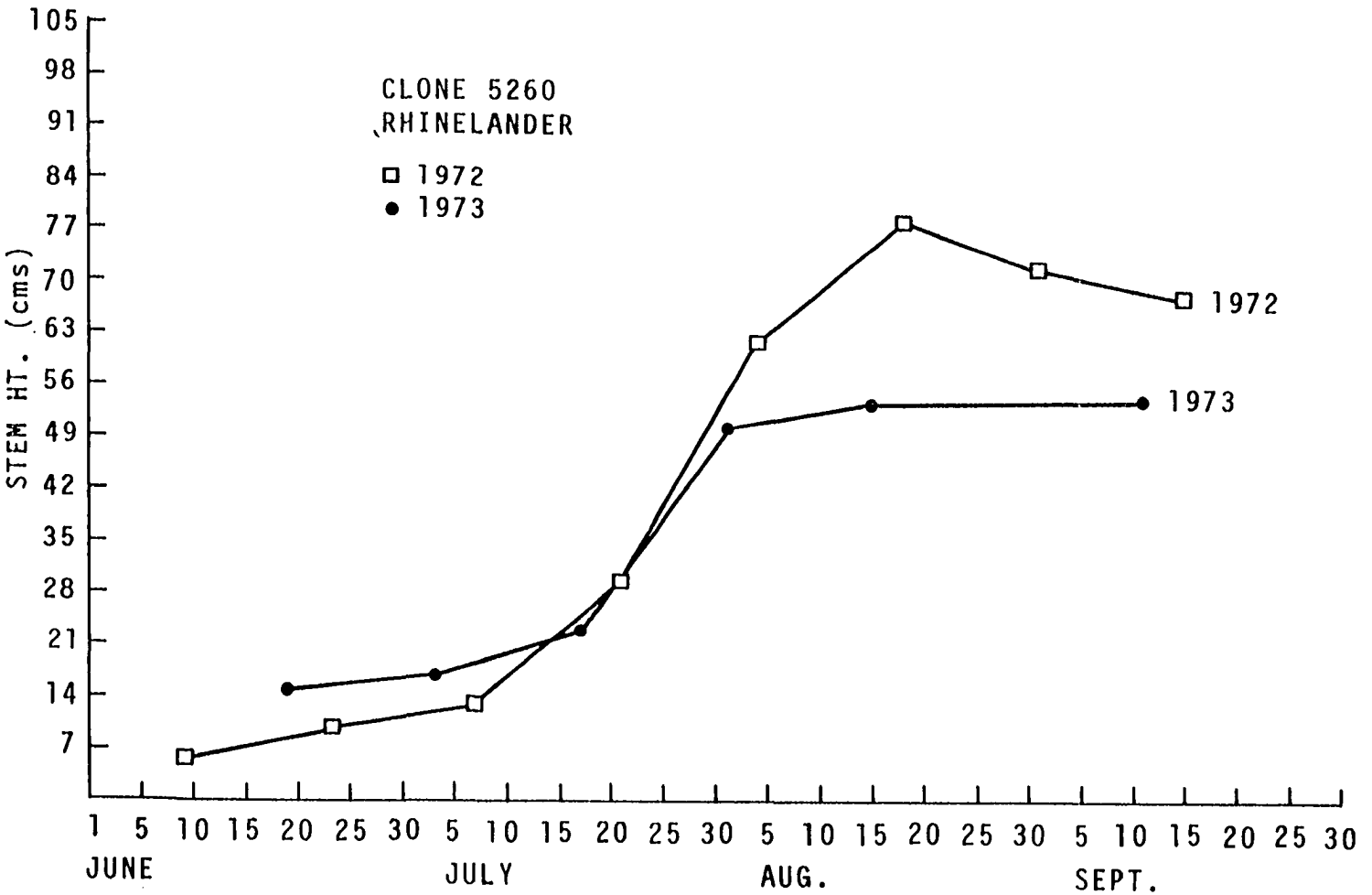
Year	Source	df	Dependent variables SH	F-value	LN	F-value
1971	Clone	2	726.87	10.42**	11988.64	24.57**
	Error (a)	14	69.73		487.84	
	Time	6	3674.70	527.03**	6579.14	39.90**
	Time x clone	12	378.48	54.28**	1733.96	10.52**
	Error (b)	123	6.97		164.89	
1972	Clone	2	14639.26	165.95**	9432.25	81.95**
	Error (a)	14	88.21		115.10	
	Time	6	17155.58		4031.90	104.85**
	Time x clone	12	2306.40	596.84**	1631.25	42.42**
	Error (b)	131	28.74	80.24**	38.45	
1973	Clone	2	4783.10	14.90**	2216.55	22.30**
	Error (a)	16	320.94		99.41	
	Time	6	17617.62	179.12**	2775.58	68.94**
	Time x clone	12	2610.69	26.54	683.49	17.00**
	Error	139	98.36		40.26	

**Significant at $P<.01$.

Rhinelander

Total height growth of clone 5260 varied between the two years that data were available; however, certain trends were evident (Figure 11). Cessation of height growth occurred about the middle of August in both years. This date coincided with the time after which there were no further increases in leaf number (Figure 14). Trends for both variables were simi-

Figure 11. Mean stem height (cms) of clone 5260, by year and measurement time, at Rhinelander. N = 9


CLONE 5260
RHINELANDER
□ 1972
● 1973
STEM HT. (cms)
105
98
91
84
77
70
63
56
49
42
35
28
21
14
7
1972
1973
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

lar. Any apparent loss in height between measurements was due to the fact that three trees per clone were harvested from the plot; their absence, therefore, contributed to a lower mean value for the residual stand.

Clone 5377 grew for a longer time than 5260 at Rhinelander, although trees from this clone also grew differently in different years (Figure 12). Trees in 1972 grew at a faster rate than those in 1973 and set bud about the first of September; those in 1973 were smaller, although they continued to grow for a slightly longer time. Increases in leaf number by the 1972 trees also ceased approximately the same time as height growth, whereas leaf production slowed greatly in 1973 about the middle of August (Figure 15). Final measurements of leaf number on 1972 plants showed them to have three times the leaves that 1973 plants possessed.

Clone 5339 also grew differently in different years. Increases in stem height occurred throughout the growing season for both years, although trees in 1973 grew more and at a faster rate than those in 1972 (Figure 13). The trend in leaf production was similar to the height growth trends for both years (Figure 16). Rankings based on final measurements of bi-monthly data agreed with rankings based on harvest data: in 1972 the ranking was 5377, 5260 and 5339 for both stem height and leaf number, whereas in 1973 it was 5377, 5339 and 5260 for both variables, although in 1973 there was very little difference in leaf number between 5377 and 5339. Again reversed rankings of 5260 and 5339 in 1972 were due to the poor growth of 5339 that year. Mean square values for first year bi-monthly measurements at Rhinelander are shown in Table 12.

Figure 12. Mean stem height (cms) of clone 5377, by year and measurement time, at Rhinelander. N = 9

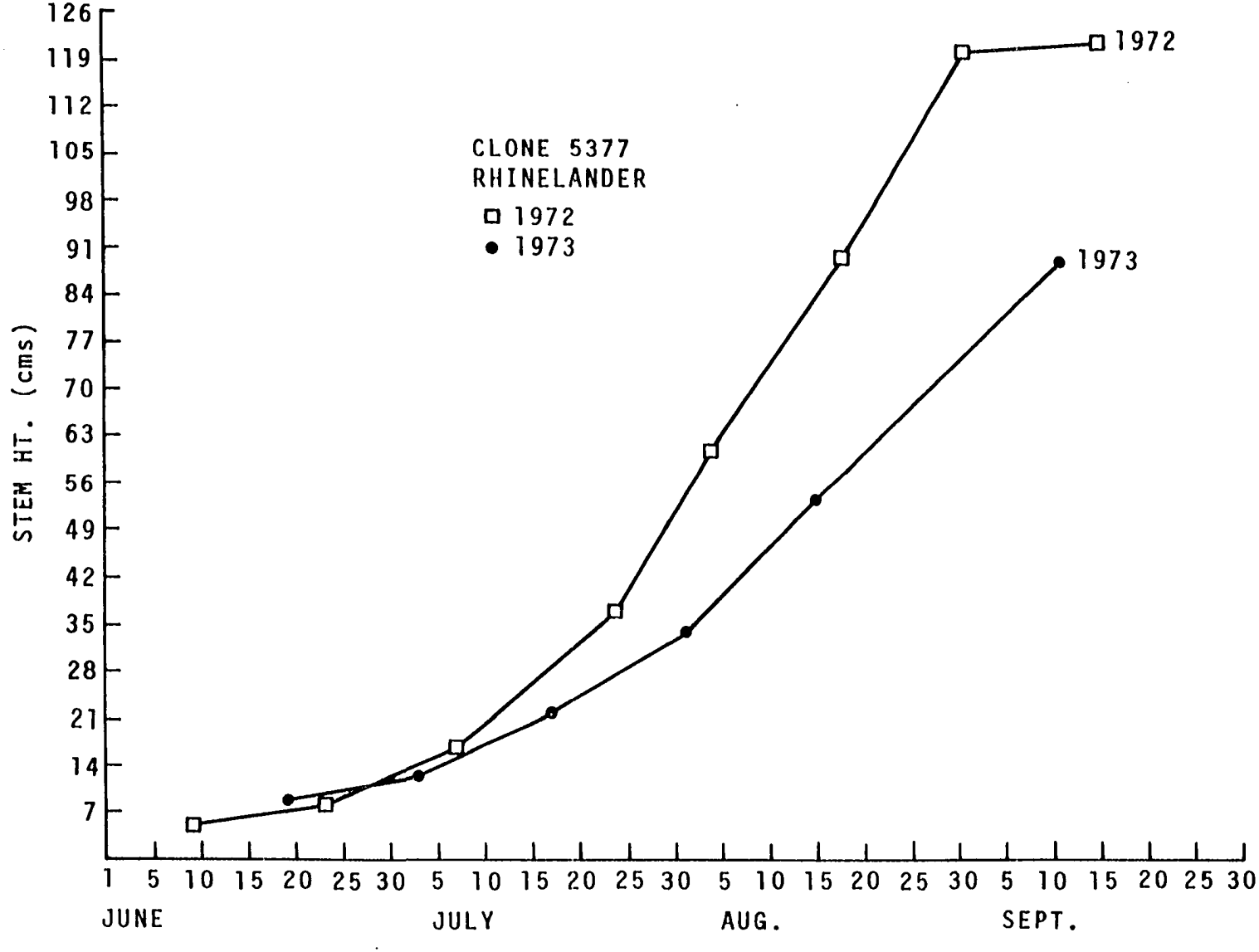

126
119
112
105
98
91
84
77
70
63
56
49
42
35
28
21
14
7
STEM HT. (cms)
CLONE 5377
RHINELANDER
1972
1973
1972
1973
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 13. Mean stem height (cms) of clone 5339, by year and measurement time, at Rhinelander. N = 9

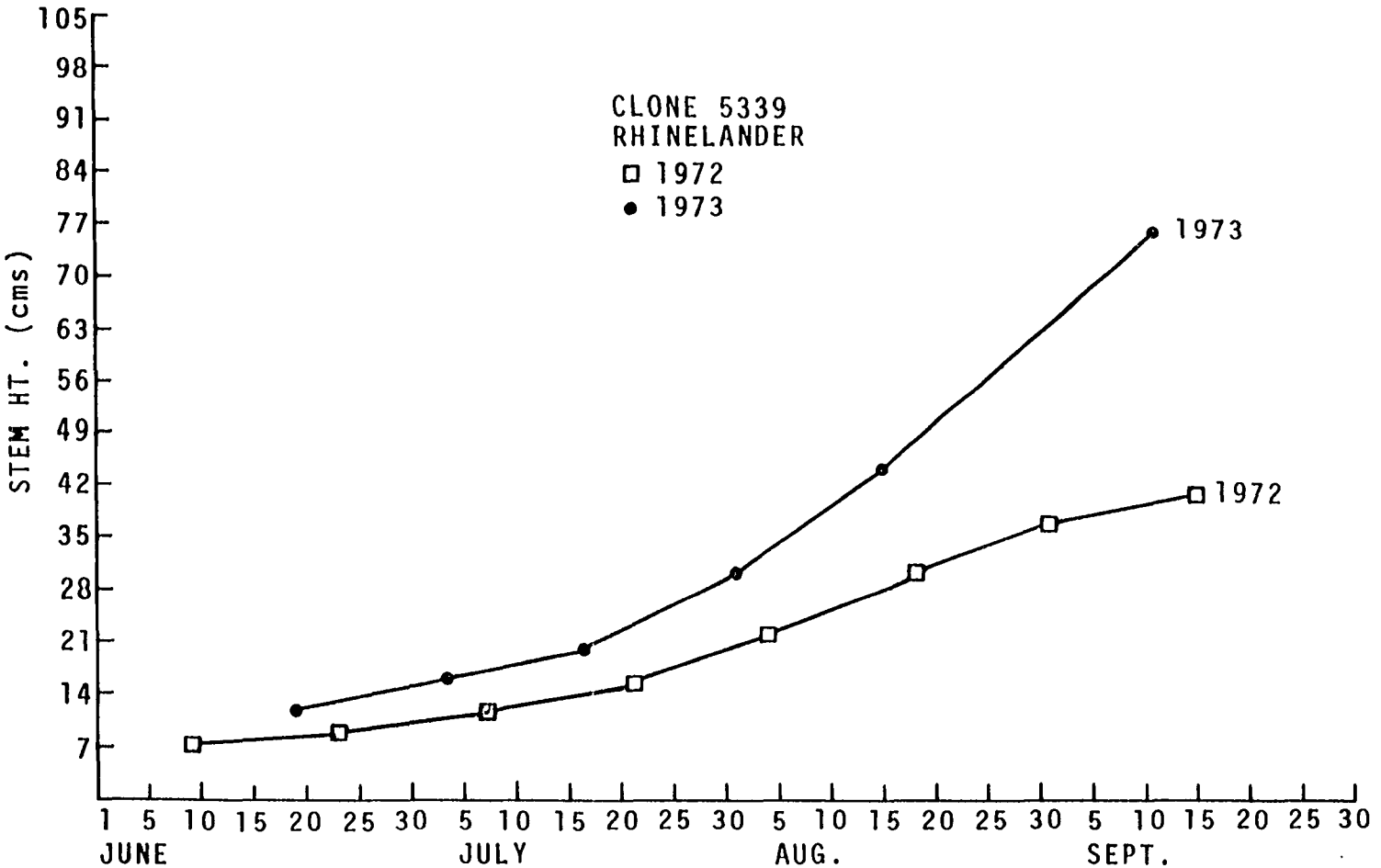

CLONE 5339
RHINELANDER
□ 1972
● 1973
STEM HT. (cms)
105
98
91
84
77
70
63
56
49
42
35
28
21
14
7
1973
1972
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 14. Mean leaf number of clone 5260, by year and measurement time, at Rhinelander. N = 9

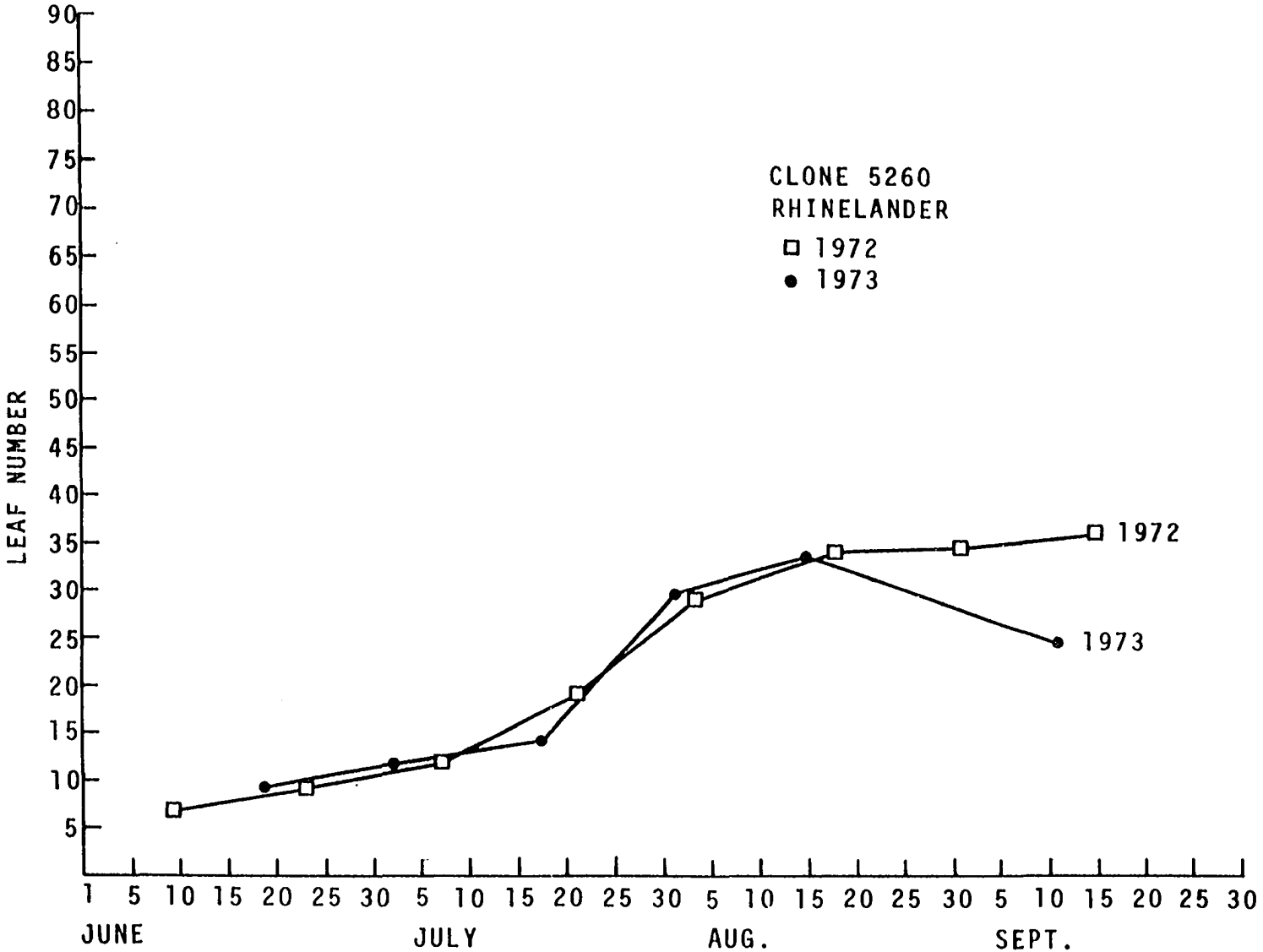

CLONE 5260
RHINELANDER
1972
1973
LEAF NUMBER
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.
1972
1973

Figure 15. Mean leaf number of clone 5377, by year and measurement time, at Rhinelander. N = 9

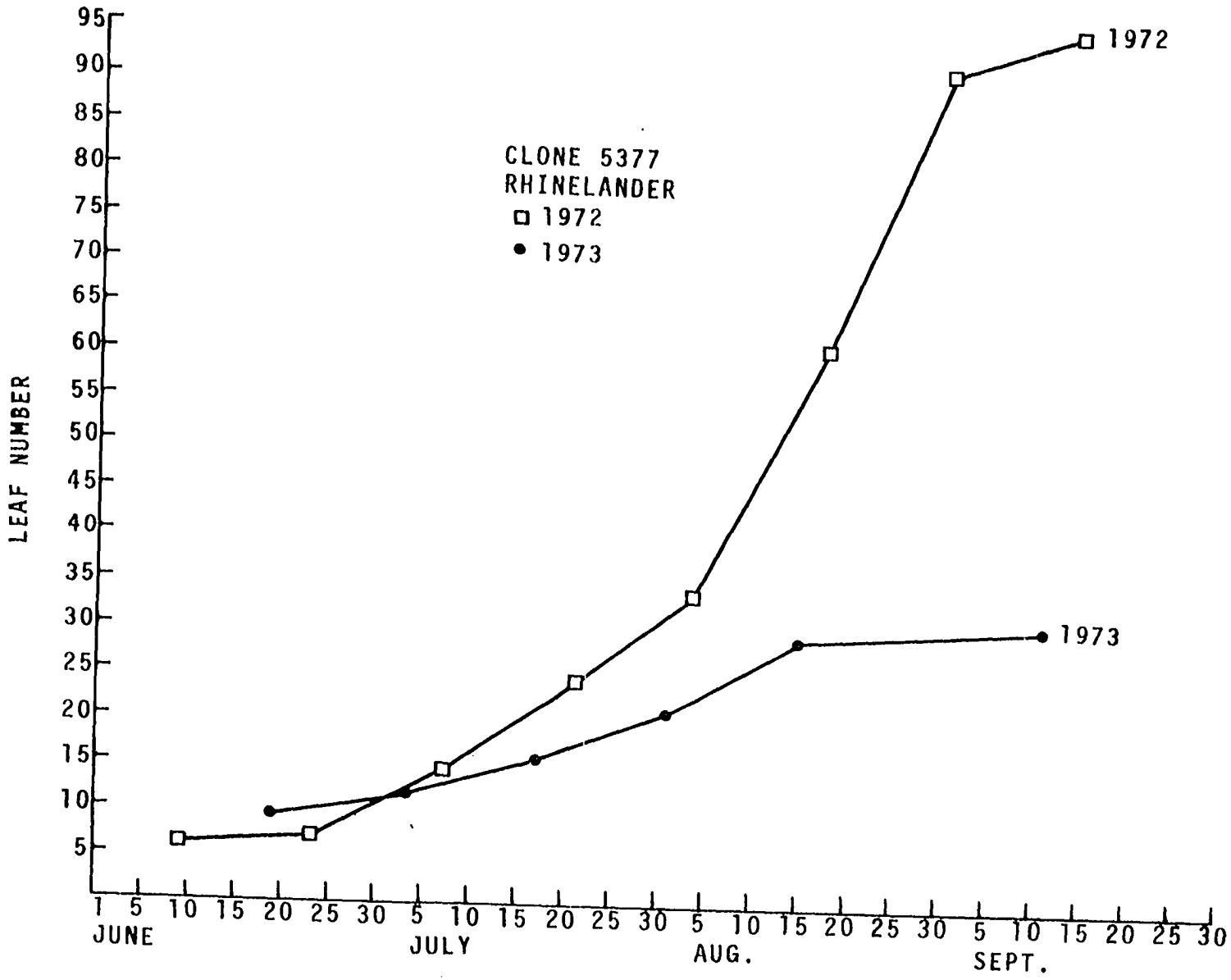

LEAF NUMBER
95
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
CLONE 5377
RHINELANDER
1972
1973
1972
1973
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 16. Mean leaf number of clone 5339, by year and measurement time, at Rhinelander. N = 9

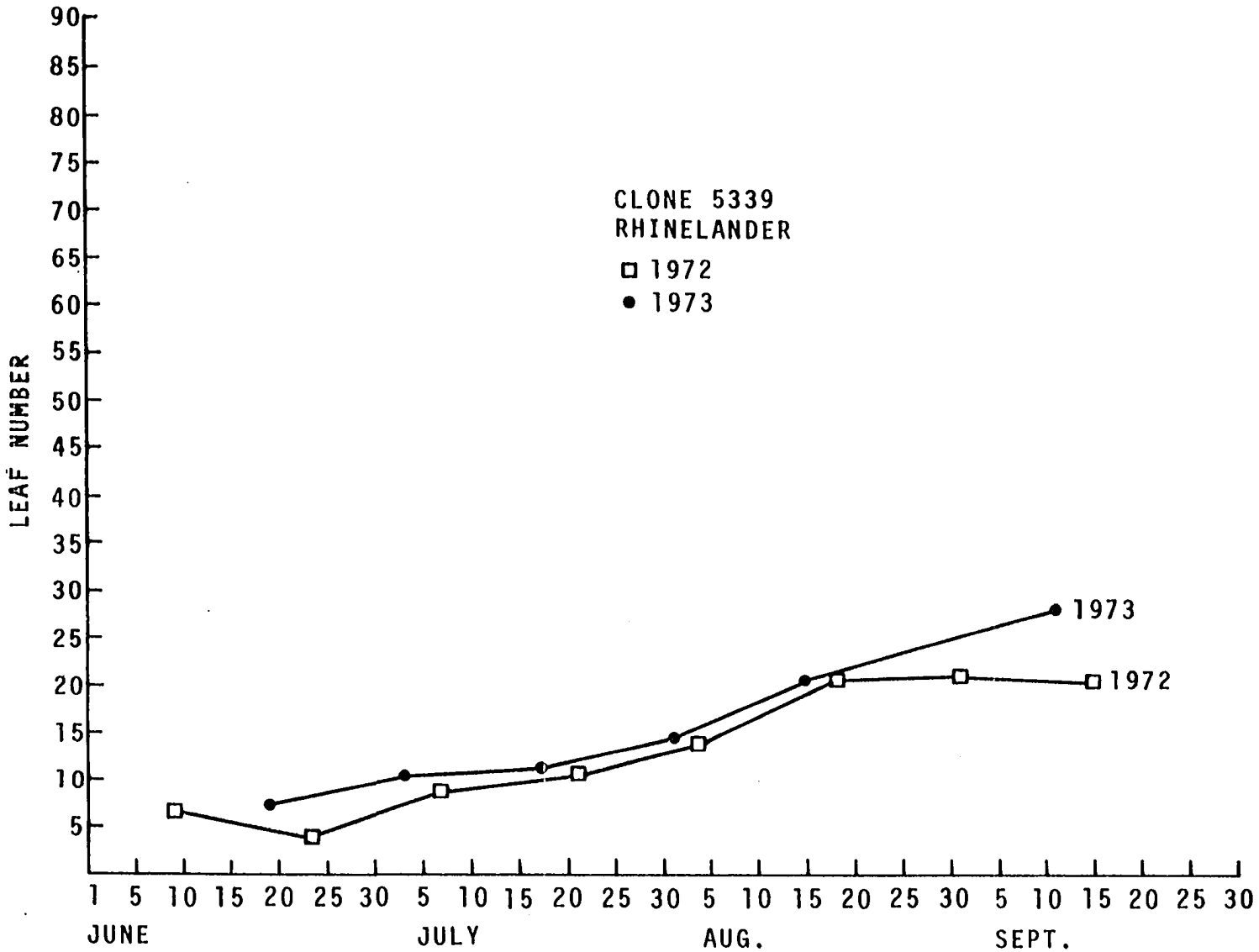

CLONE 5339
RHINELANDER
□ 1972
● 1973
LEAF NUMBER
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
1973
1972
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Table 12. Mean squares and F-values by variable for first year bi-monthly measurements at Rhinelander

Year	Source	df	Dependent variables SH	F-value	LN	F-value
1971	Clone	-	--	--	--	--
	Error (a)	-	--	--	--	--
	Time	-	--	--	--	--
	Time x clone	-	--	--	--	--
	Error (b)	-	--	--	--	--
1972	Clone	2	18185.76	39.03**	12990.68	16.79**
	Error (a)	14	466.00		773.79	
	Time	7	22472.67	354.90**	8066.90	38.04**
	Time x clone	14	2924.18	46.18**	2320.41	10.94**
	Error (b)	154	63.32		212.04	
1973	Clone	2	130.30	0.73	381.06	13.33**
	Error (a)	14	178.06		28.59	
	Time	5	15054.19	616.64**	1851.80	104.39**
	Time x clone	10	821.44	33.65**	122.58	6.91**
	Error (b)	120	24.41		17.74	

**Significant at $P<.01$.

Clonal Comparison of Bi-monthly Data between Locations

Clone 5260 set bud before the end of the growing season at both locations, although it grew for a slightly longer time at Rhinelander.

Clone 5377 grew well throughout the growing season at both locations. There was less variability between replications with respect to stem height at Ames, whereas much variation occurred with respect to leaf production at both locations.

Growth of 5339 differed greatly in different years at both locations. It did not grow well at either location in 1972; growth in 1973 was only slightly better at the Rhinelander site, based on the final bi-monthly

measurement data. Any variance between bi-monthly measurement data and harvest data was not large enough to disrupt the agreement in rankings. At both locations 5377 ranked in first place for both variables measured. Clone 5260 ranked in last place for both variables for two years (1971, 1973 in Ames and one year in Rhinelander (1973).

Field Growth: Bi-monthly Measurement of Second- and Third-Year-Old Stem Height Growth

Growth in stem heights for second- and third-year-old 5260 was similar for all the years measured at the Ames location (Table 13 and Figures 17, 18 and 19). Increases in height growth were essentially complete by June 21, the longest day of the year. Last measurement values for 5260 on two-year-old material measured in 1972 and 1973 differed by only 30 cm. In all cases for two- and three-year-old growth, 5260 growth was considerably smaller than 5377 and usually much smaller than 5339.

The trend for second year 5377 trees was similar for trees planted in 1971 and 1972. Generally the trees grew throughout both growing seasons. Mean stem height values differed by only 15 cm between the two years for the final measurement date. Three-year-old 5377 trees slowed markedly in height growth by the first part of July.

Clone 5339 had the same growth trend for both second year seasons. However, trees measured in 1973 (planted in 1972) were much smaller than those measured in 1972 (planted in 1971) due to the poor first year growth of 5339 in 1972. Rankings of two-year-old trees in 1972 based on the last measurement data were 5339, 5377 and 5260. For 1973 measurements the ranking was 5377, 5339 and 5260. Change in the position occupied by clone 5339 was again due to poor first year growth.

Table 13. Means for stem height (in cms) by clone, time and year for second and third year bi-monthly measurements at Ames

Year planted	Year measured	Time[a]	Clone 5260	Clone 5377	Clone 5339
1971[b]	1972	0	59.5	100.9	109.5
		1	96.9	123.9	134.5
		2	113.0	152.0	155.8
		3	115.3	181.2	174.5
		4	115.3	215.9	196.8
		5	115.3	228.7	218.0
		6	115.3	240.0	246.0
		7	115.3	242.6	252.3
1971[b]	1973	0	115.3	242.6	252.3
		1	186.5	284.4	300.7
		2	202.2	305.4	315.3
		3	204.8	320.2	343.3
		4	205.2	327.2	378.3
		5	205.2	329.6	431.9
1972[b]	1973	0	57.2	110.0	32.8
		1	85.0	161.2	51.0
		2	85.2	182.3	64.3
		3	85.2	210.2	81.0
		4	85.2	239.7	99.3
		5	85.2	257.7	113.7

[a]Time 0 = last measurement taken previous year.

[b]N varies from 3 to 9.

Rankings based on last measured bi-monthly data for three-year-old trees showed 5339 to be firmly in first place followed by 5377 and 5260. Three-year-old 5339 continued to grow throughout the season unlike the other two clones.

Mean square values for second and third year bi-monthly growth measurements at Ames are shown in Table 14.

Figure 17. Mean stem height (cms), by year and measurement time, for two-year-old trees at Ames (planted 1971, measured 1972). Circled point on this and subsequent figures is mean of last measurement taken in year planted on same trees

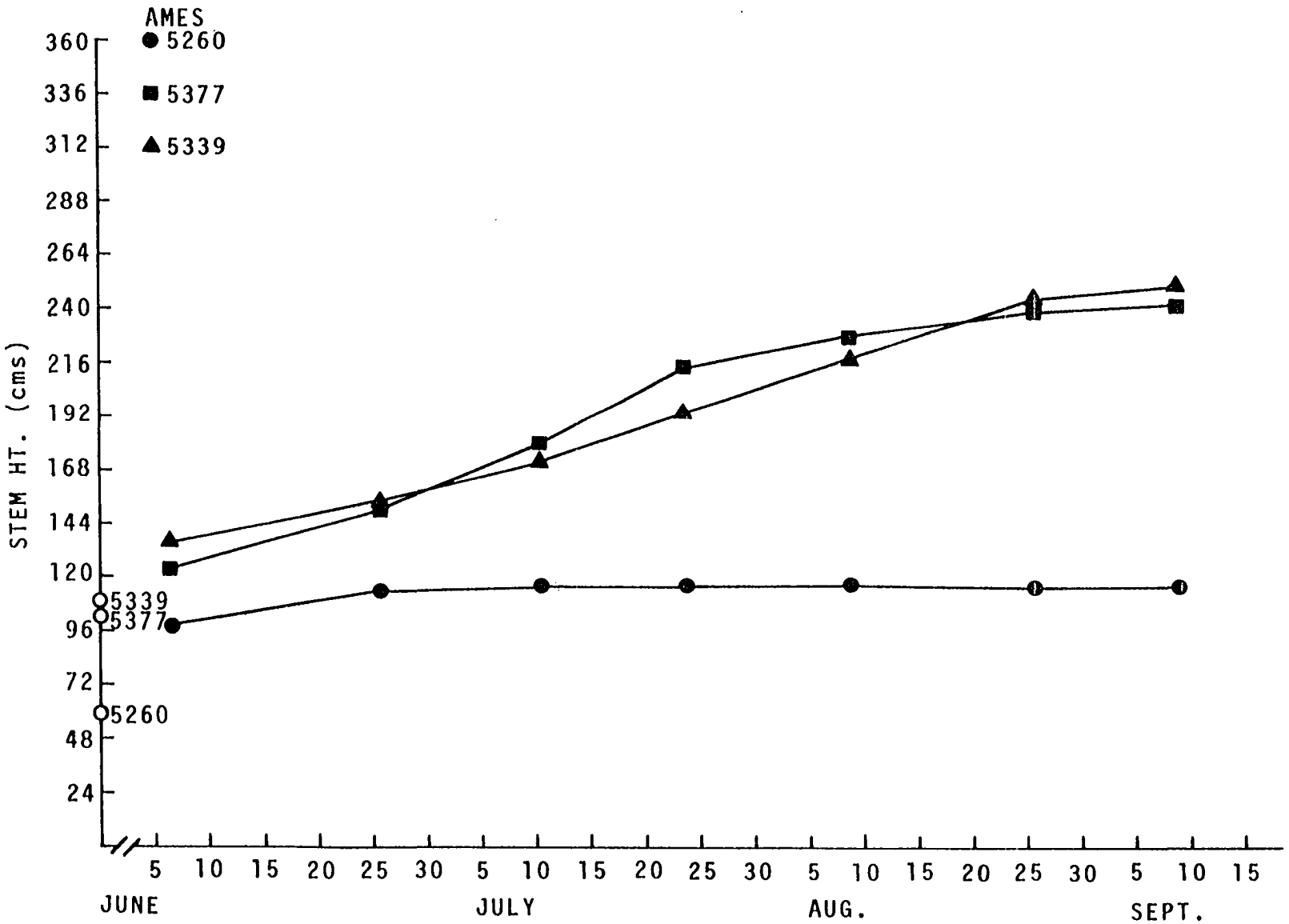

AMES
● 5260
■ 5377
▲ 5339
360
336
312
288
264
240
216
192
168
144
120
96
72
48
24
STEM HT. (cms)
5339
5377
5260
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15
JUNE
JULY
AUG.
SEPT.

Figure 18. Mean stem height (cms), by year and measurement time, for two-year-old trees at Ames (planted 1972, measured 1973)

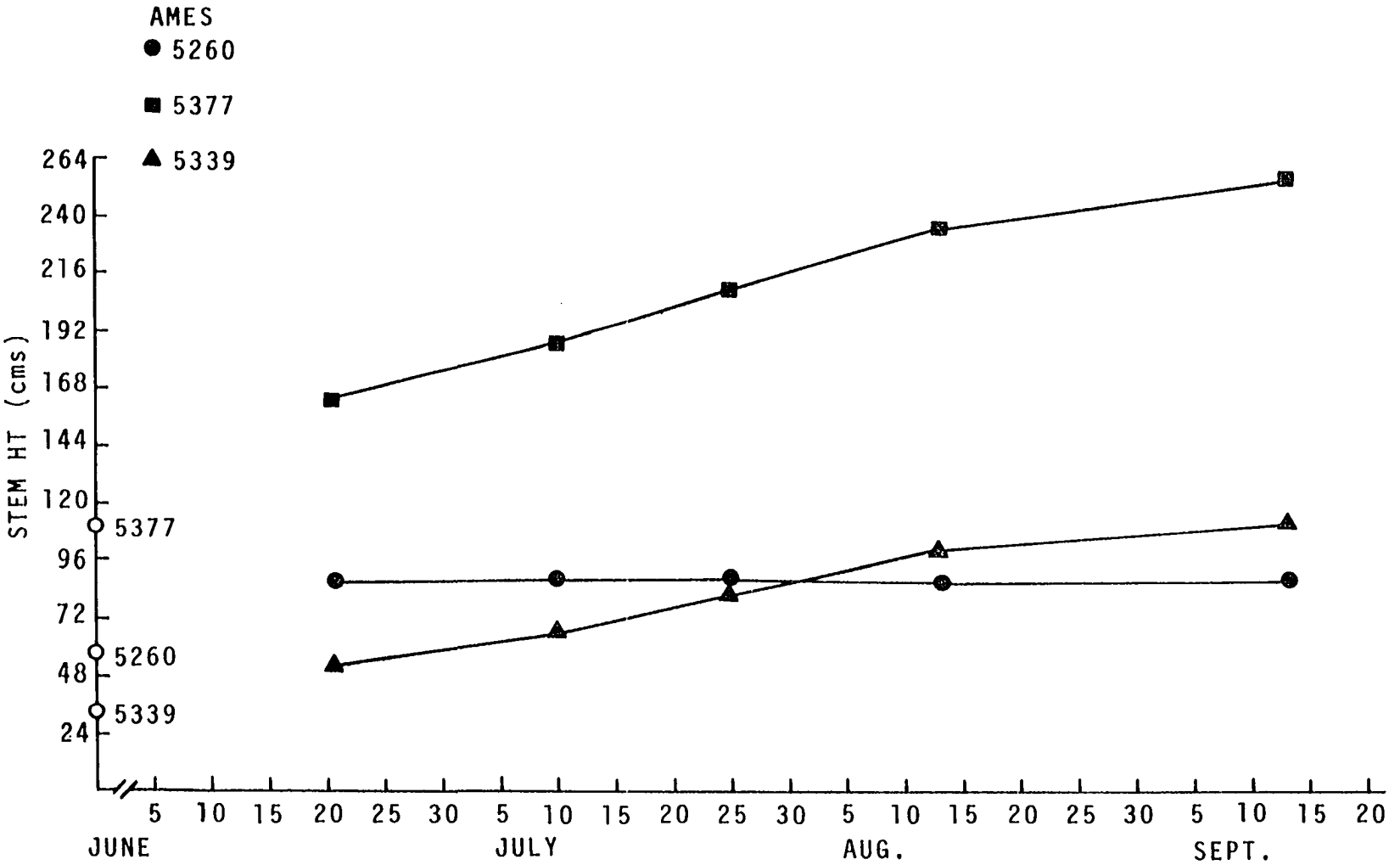

AMES
● 5260
■ 5377
▲ 5339
STEM HT (cms)
264
240
216
192
168
144
120
96
72
48
24
5377
5260
5339
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20
JUNE
JULY
AUG.
SEPT.

Figure 19. Mean stem height (cms), by year and measurement time, for three-year-old trees at Ames (planted 1971, measured 1973). Circled point mean of last measurement taken in 1972 on same trees

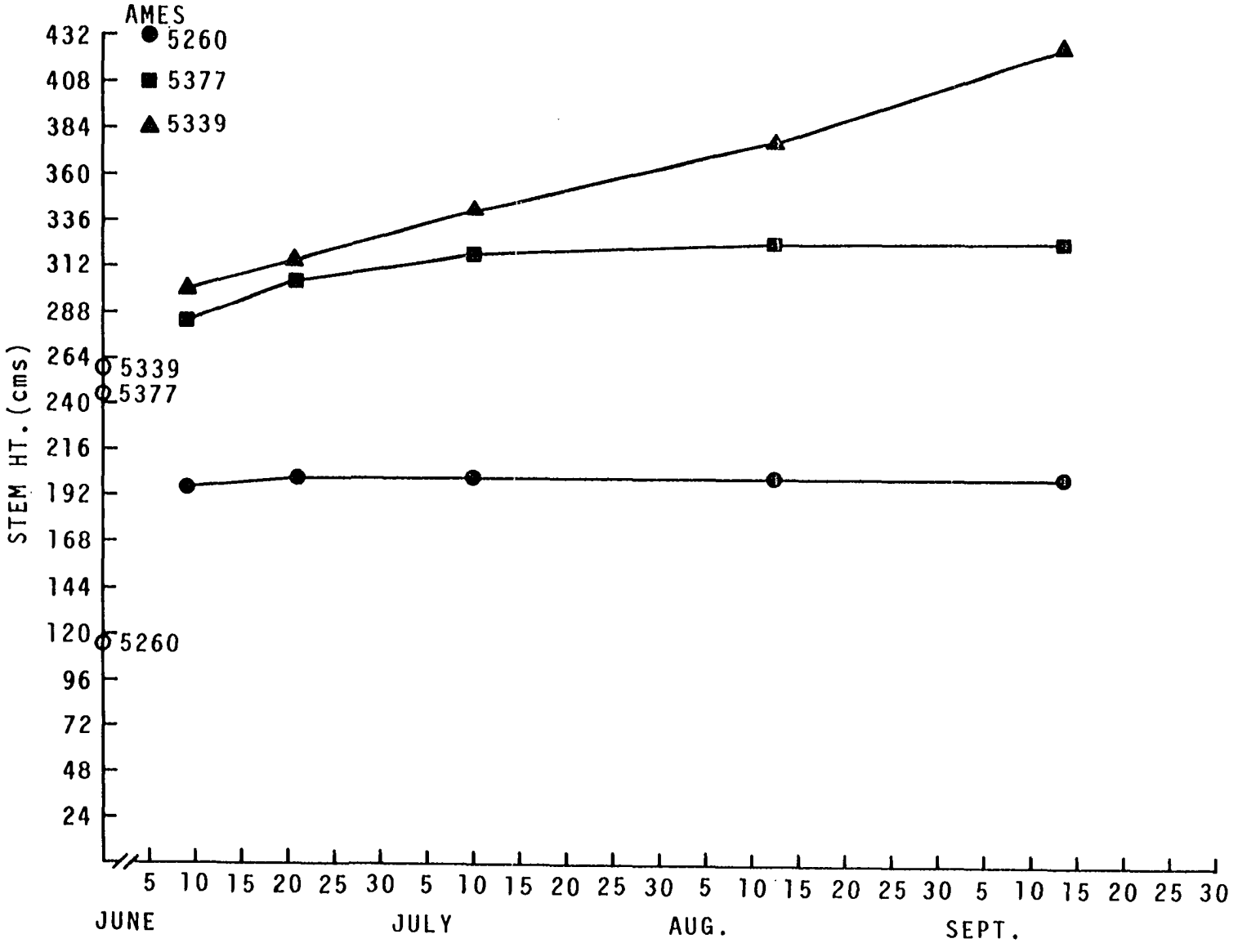

AMES
5260
5377
5339
STEM HT. (cms)
432
408
384
360
336
312
288
264
240
216
192
168
144
120
96
72
48
24
5339
5377
5260
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Table 14. Mean squares and F-values for stem height for second and third year bi-monthly measurements at Ames

Year planted	Year measured	Source	df	Dependent variables MS	Dependent variables F-values
1971	1972	Clone	2	80738.0	436.4**
		Time	6	13026.5	70.4**
		Time x clone	12	2952.7	16.0**
		Error	68	185.0	
1971	1973	Clone	2	140382.03	688.33**
		Time	4	8173.34	38.91**
		Time x clone	8	2384.50	11.35**
		Error	46	210.05	
1972	1973	Clone	2	132367.74	1534.16**
		Time	4	6395.47	74.12**
		Time x clone	8	2394.85	27.76**
		Error	51	86.28	

**Significant at $P<.01$.

At Rhinelander two-year-old 5260 increased in stem height in both second year growing seasons until the first of August when the trees set bud (Table 15 and Figures 20 and 21). Trees planted in 1972 (measured 1973), however, showed greater final height growth, probably because trees in 1971 (measured 1972) were not planted until July of that year. Three-year-old clone 5260 ceased height growth by the middle of July (Figure 22).

Two-year-old 5377 trees also showed the same trends for both years measured, although the trees planted in 1971 set bud slightly before those planted in 1972. Again final height values for 1972 plants were greater than those in 1971. Three-year-old 5377 trees grew in height similar to two-year-old plants. Greatest increases in height were made in the first half of the growing season for three-year-old material.

Table 15. Means for stem height (in cms) by clone, time and year for second and third year bi-monthly measurements at Rhinelander

Year planted	Year measured	Time[a]	Clone 5260	Clone 5377	Clone 5339
1971[b]	1972	0	--	--	--
		1	71.3	90.3	88.6
		2	84.6	107.3	104.4
		3	102.0	138.1	122.8
		4	121.1	172.2	141.9
		5	125.6	200.6	159.0
		6	125.6	229.2	177.2
		7	125.6	229.8	180.2
1971[b]	1973	0	125.6	229.8	180.2
		1	186.4	254.2	202.0
		2	207.3	285.8	227.4
		3	211.0	317.8	246.2
		4	211.3	353.3	271.0
		5	211.6	386.0	328.6
1972[b]	1973	0	73.8	120.8	44.4
		1	136.0	158.3	61.4
		2	163.0	183.8	73.4
		3	179.3	215.8	87.6
		4	180.7	251.2	109.8
		5	181.2	285.2	133.8

[a]Time 0 = last measurement taken in previous year.

[b]N varies from 5 to 9.

The trend for height growth of 5339 was also similar for two-year-old trees. Three-year-old 5339 trees grew steadily throughout the growing season. Rankings based on final bi-monthly measurement data showed 5377 to be in first place all three years followed by 5339 and 5260, respectively, for two-year growth measured in 1972 and 5260 and 5339 for two-year growth measured in 1973. The ranking for three-year-old trees was 5377, 5339 and

Figure 20. Mean stem height (cms), by year and measurement time, for two-year-old trees at Rhinelander (planted 1971, measured 1972)

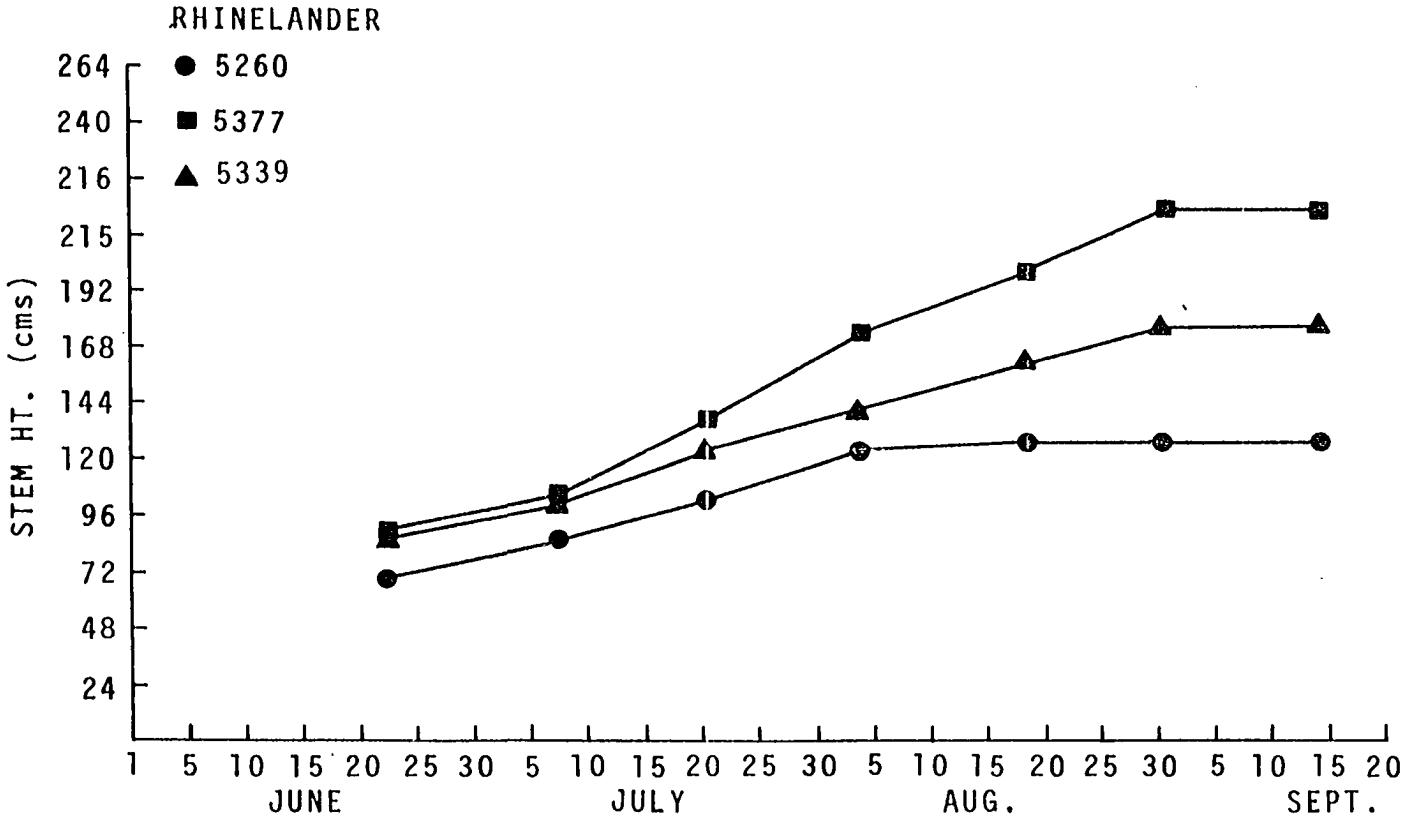

RHINELANDER
● 5260
■ 5377
▲ 5339
STEM HT. (cms)
264
240
216
215
192
168
144
120
96
72
48
24
1 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20
JUNE
JULY
AUG.
SEPT.

Figure 21. Mean stem height (cms), by year and measurement time, for two-year-old trees at Rhinelander (planted 1972, measured 1973)

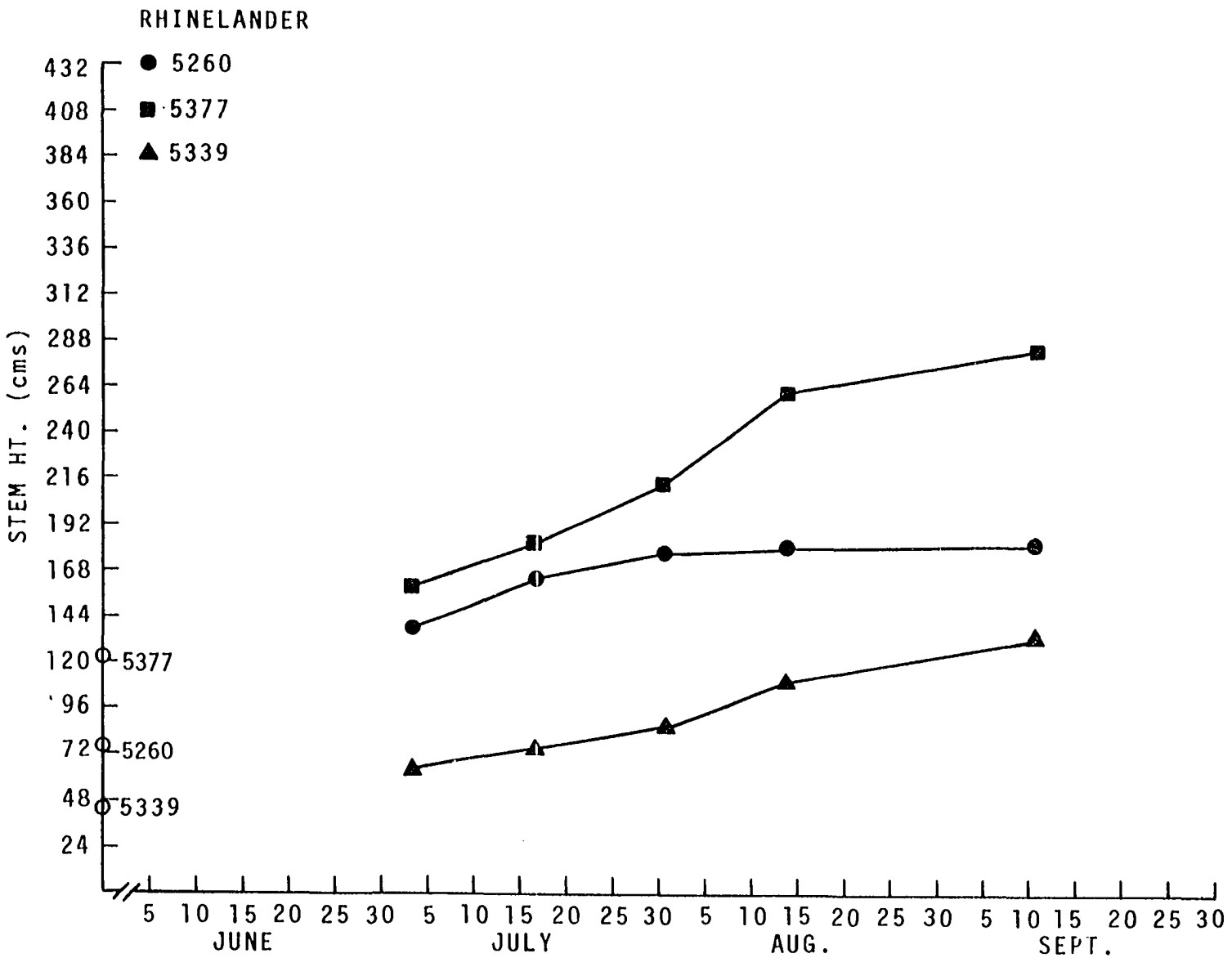
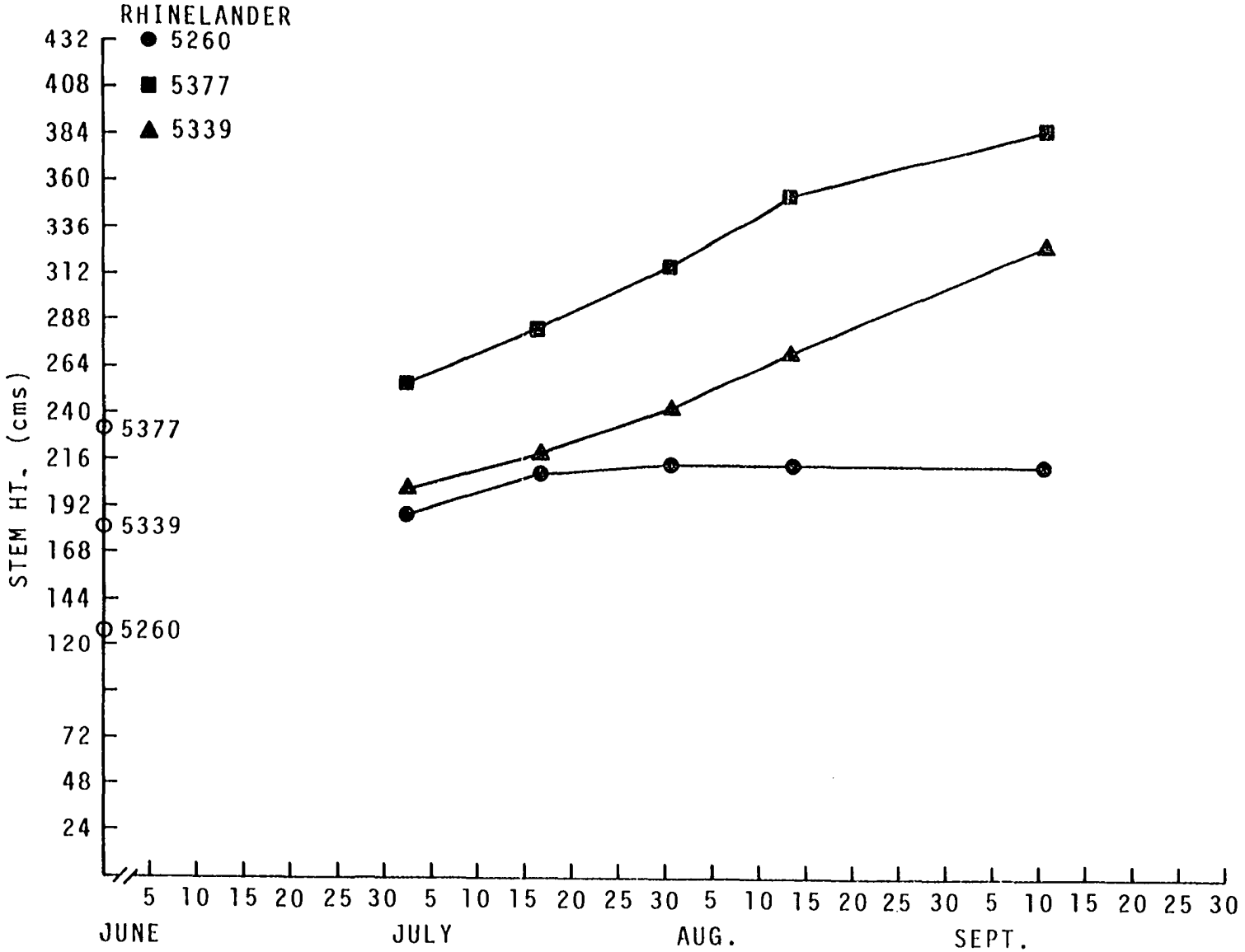

RHINELANDER
● 5260
■ 5377
▲ 5339
STEM HT. (cms)
432
408
384
360
336
312
288
264
240
216
192
168
144
120
96
72
48
24
5377
5260
5339
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

Figure 22. Mean stem height (cms), by year and measurement time, for three-year-old trees at Rhinelander (planted 1971, measured 1973). Circled point mean of last measurement taken in 1972 on same trees


RHINELANDER
● 5260
■ 5377
▲ 5339
STEM HT. (cms)
432
408
384
360
336
312
288
264
240
216
192
168
144
120
72
48
24
5377
5339
5260
5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20 25 30
JUNE
JULY
AUG.
SEPT.

5260. Analysis of variance of old growth bi-monthly measurements at Rhinelander is shown in Table 16.

Table 16. Mean squares and F-values for stem height for second and third year bi-monthly measurements at Rhinelander

Year planted	Year measured	Source	df	MS	F-values
1971	1972	Clone	2	54598.10	187.48**
		Time	6	38743.89	133.05**
		Time x clone	12	3004.24	10.32**
		Error	154	291.21	
1971	1973	Clone	2	115978.10	424.72**
		Time	4	30133.56	110.35**
		Time x clone	8	5292.45	19.38**
		Error		273.07	
1972	1973	Clone	2	84061.84	460.59**
		Time	4	17462.13	95.67**
		Time x clone	8	2074.08	11.36**
		Error	61	182.51	

**Significant at $P<.01$.

Clonal Comparisons between Years for Second- and Third-Year-Old Bi-monthly Measurements

Growth behavior of 5260 was similar at both locations in that it grew for only the first part of the season and then set bud; clone 5260 grew for a slightly longer time in Rhinelander, however.

Growth trends for two-year-old 5377 trees were similar for both years measured at both locations. Trends for the growth of three-year-old trees differed between locations; those growing at Ames set bud about a month earlier than those at Rhinelander.

Clone 5339 grew in the same relative fashion at both locations for all the years measured but final heights differed markedly between sites.

Values were averaged for the two replications of two-year-old growth measurements at each location. Using this as a basis of comparison, it was apparent that after two years 5260 grew better in Rhinelander. Clone 5377 grew approximately the same at both locations and 5339 grew better at Ames. Final bi-monthly measurement of three-year-old trees showed that 5260 grew about the same at both locations, 5377 grew slightly better at Rhinelander and 5339 grew much better at Ames. Thus, the relative comparisons determined by using bi-monthly measurements were in agreement with those found using harvest data. Rankings based on final bi-monthly measurements after two years generally agreed with rankings based on two-year-old harvest data at both locations, not only for the one common variable, stem height, but also for the two other variables measured at harvest time, namely, stem diameter and stem dry weight. Rankings for three-year-old trees were exactly the same for all variables when harvest and final bi-monthly data were compared at both locations.

Growth Chamber Growth: Harvest Data

Differences in final height growth in the controlled environment under the 13-hour photoperiod were very small, but with increasing photoperiod, the differences between clones became more apparent (Table 17 and Figure 23). Under a 14-hour photoperiod, 5339 increased markedly in height with a smaller but significant increase in height also occurring for clone 5377 in comparison to the heights under the 13-hour photoperiod. Growth in height of 5260 under a 14-hour photoperiod differed very little from that

Table 17. Means by variable, clone and photoperiod for growth chamber harvest data[a]

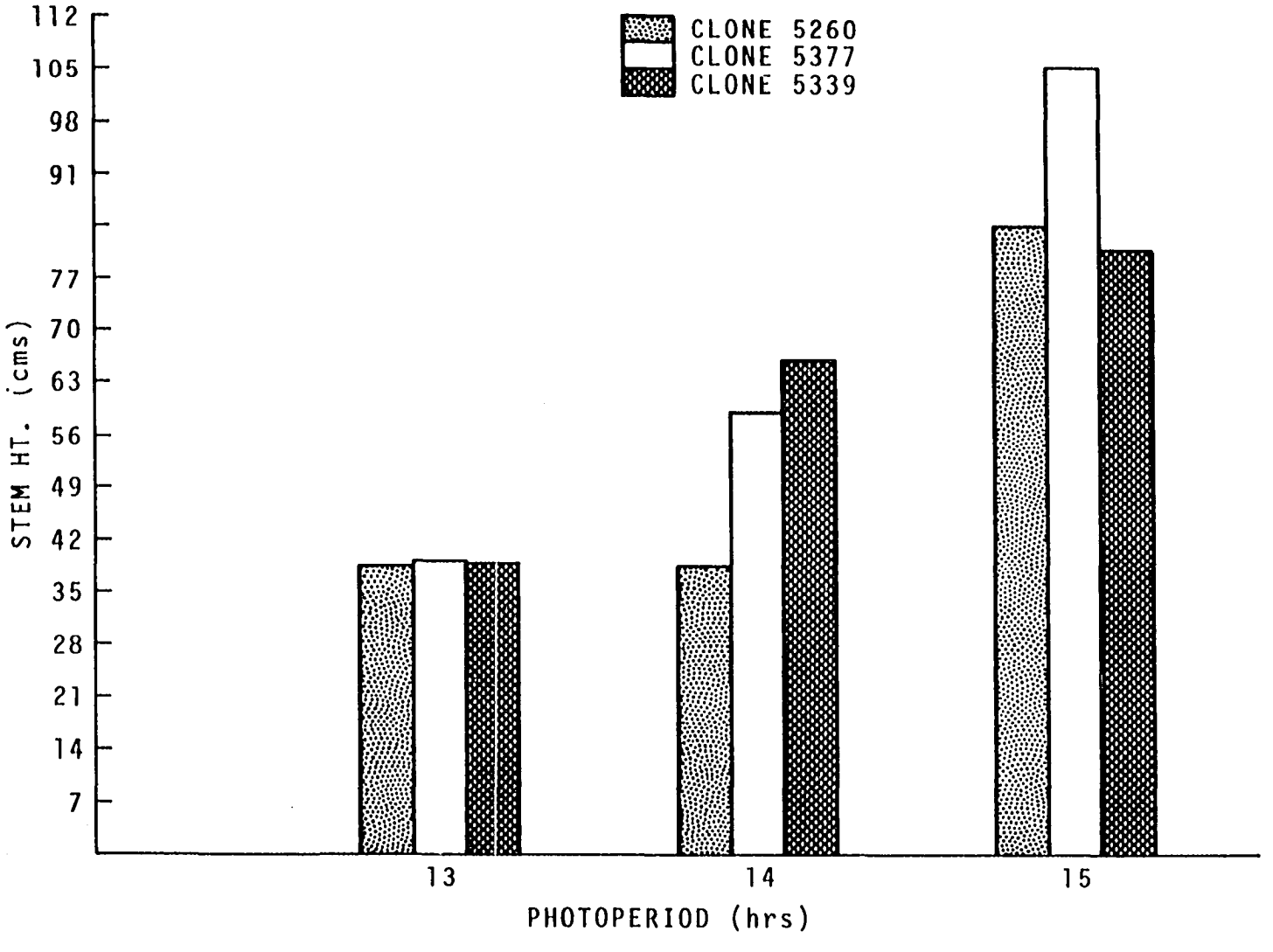
Photoperiod (hrs)	Clone	Dependent variables SH (cm)	SD (in)	LW (gm)	SW (gm)	TTW (gm)	LA_2 (cm^2)	LF
13	5260	38.56	0.309	4.44	2.41	6.85	687.3	15.0
13	5377	39.29	0.352	7.02	2.82	9.84	1073.7	19.3
13	5339	38.86	0.325	6.95	2.36	9.31	1159.2	18.2
14	5260	38.72	0.414	5.21	2.48	7.82	808.9	17.8
14	5377	59.06	0.833	13.37	6.28	19.62	2298.3	29.6
14	5339	68.25	0.324	8.68	4.24	12.99	1443.7	22.3
15	5260	84.64	0.619	11.49	7.10	18.59	1806.4	26.9
15	5377	105.22	0.910	19.82	12.38	32.20	5208.9	34.4
15	5339	80.84	0.427	13.41	6.87	20.28	3337.7	25.5

[a]N = 12 (3 trees/clone/photoperiod x 4 replications).

observed in the 13-hour treatment; in both photoperiods, 5260 grew for only about 20 days and then set bud. Under the 15-hour photoperiod, however, all clones grew throughout the growing period. The largest percentage increase in height in the 15-hour photoperiod was made by 5260 followed by 5377 and then 5339, as compared to growth in the 14-hour treatment. Final height under the 14-hour photoperiod was greatest for 5339, while under the 15-hour photoperiod the final height was greatest for 5377.

Differences in stem diameter among the three clones were again small under the 13-hour photoperiod; differences between the clone with the largest diameter (5377) and the smallest diameter (5260) were only 13%. With increasing photoperiod, clonal differences in diameter growth were magnified. Under the 14-hour photoperiod, the average diameter of 5377 trees

Figure 23. Mean stem height (cms) by clone and photoperiod. N = 2


CLONE 5260
CLONE 5377
CLONE 5339
STEM HT. (cms)
112
105
98
91
77
70
63
56
49
42
35
28
21
14
7
13
14
15
PHOTOPERIOD (hrs)

more than doubled (137% increase) as compared to the 13-hour photoperiod; 5260 increased somewhat in diameter (34% increase), while the diameter of 5399 was almost identical to the 13-hour values. Under the 15-hour treatment, the largest increase in diameter was made by 5260 (50%) although all clones showed diameter increases. Clone 5377 showed the largest final diameter measurement and 5339 the smallest under both the 14- and 15-hour photoperiods.

Average leaf dry weight per plant was smallest under the 13-hour photoperiod and increased with longer photoperiods for all clones. Under the 14-hour photoperiod, 5377 increased significantly in leaf dry weight (91%) with smaller increases shown by 5399 (25%) and 5260 (18%), as compared to the 13-hour values. Under the 15-hour photoperiod, 5260 increased by far the most in average leaf dry weight per plant (121%), with an approximately equal increase shown by 5339 and 5377. Clone 5377 showed the largest average leaf dry weight per plant and 5260 the smallest values under both the 14- and 15-hour photoperiods.

Average leaf number was smallest under the 13-hour treatment for all clones; clonal differences were also smallest in this treatment. Leaf numbers by clone increased with increased photoperiod, although the largest differences among clones were observed in the 14-hour treatment. Increases in leaf number by clone and photoperiod were similar to increases in other variables; that is, 5377 increased more in leaf number percentage between the 13-hour and 14-hour treatment, whereas 5260 made largest percentage increase between the 14-hour and 15-hour photoperiod.

The average individual leaf weight was approximately equal among clones under the 13-hour treatment (0.35 gm). Under the 14-hour treatment,

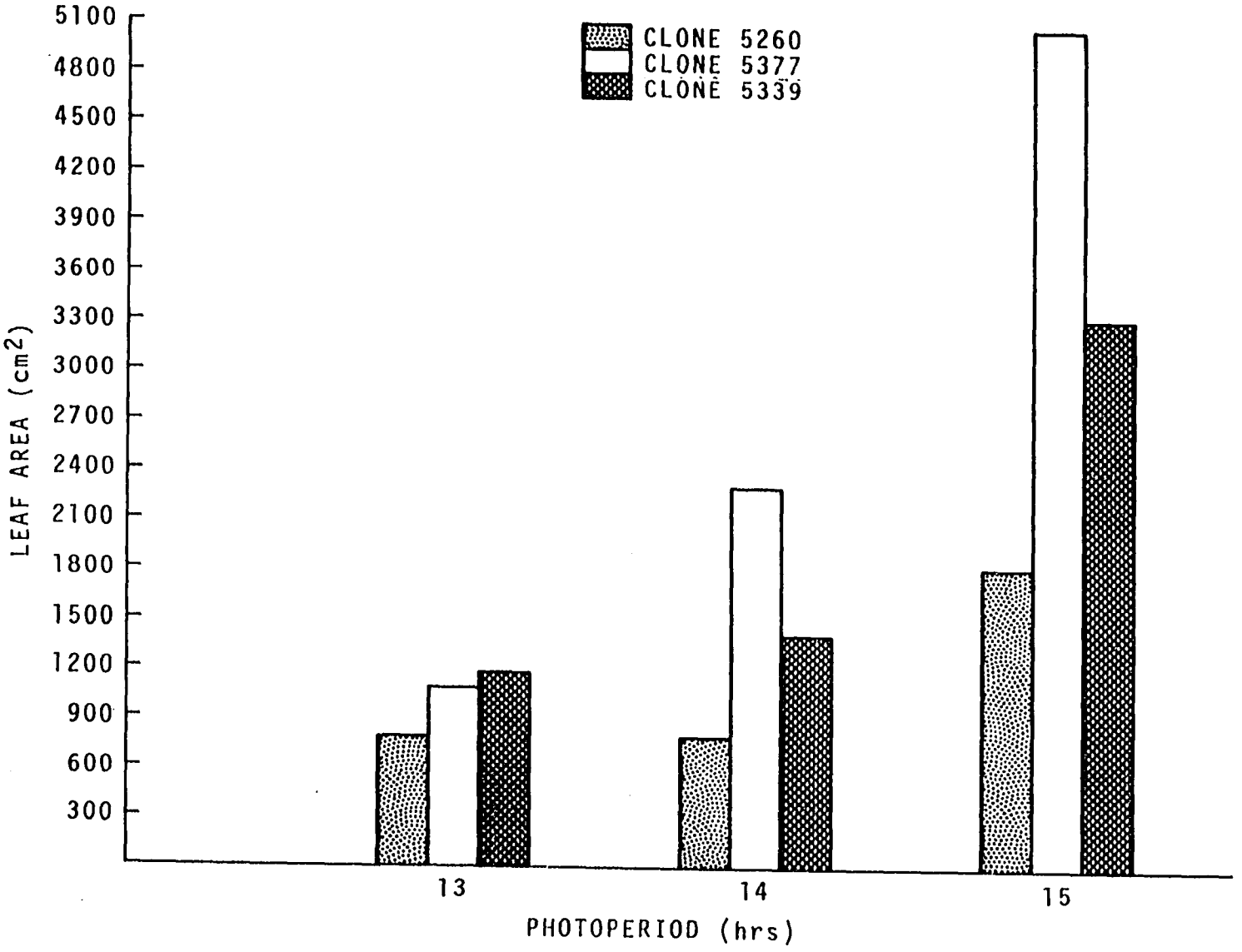
this value was similar for 5260 and 5339, with an increase by 5377 (0.46 gm); in the 15-hour treatment, all clones increased in approximately equal amounts over the 14-hour values, with 5377 showing the largest average leaf weight (0.58 gm) followed by 5339 (0.53 gm) and finally by 5260 (0.43 gm).

Trends for stem weight growth were similar to those previously presented for other variables. Small differences among clones occurred under the 13-hour photoperiod, with greater final values and clonal differences apparent with increasing photoperiod. Clone 5260 again showed little increase in stem weight (.03%) in the 14-hour photoperiod compared to the 13-hour value, while 5377 showed the greatest increase (123%) followed by 5339 (80%). In the 15-hour treatment, however, 5260 increased 187% over the 14-hour value with smaller but significant increases being made by 5377 (98%) and 5339 (62%).

Final stem weight values were largest for 5377 followed by 5339 and 5260, respectively, in the 14-hour photoperiod and by 5260 and 5339, respectively, in the 15-hour photoperiod. Results for total top dry weight growth paralleled those for average leaf dry weight and stem weight. Total top dry weight by clone increased with increasing photoperiod, with 5377 showing the greatest values under all three photoperiods. Again clonal differences increased as the length of the photoperiod increased.

Growth trends for average total leaf area per plant were unlike those for any other variable measured (Figure 24). Differences among clones and final amount of leaf area for each clone were smallest under the 13-hour photoperiod and increased with longer photoperiods, but the rate of increase for the clones differed from other variables. Between the 13-hour and 14-hour photoperiods, 5377 increased in leaf area by 114%, with smaller

Figure 24. Mean leaf area (cm^2) by clone and photoperiod. N = 12


CLONE 5260
CLONE 5377
CLONE 5339
LEAF AREA (cm²)
5100
4800
4500
4200
3900
3600
3300
3000
2700
2400
2100
1800
1500
1200
900
600
300
13
14
15
PHOTOPERIOD (hrs)

increases by clones 5339 (25%) and 5260 (18%). Under the 15-hour treatment, however, all clones increased significantly in total leaf area per plant. Specific amounts of increase were 124, 127 and 132% for 5260, 5377 and 5339, respectively.

Largest clonal differences occurred in the 15-hour treatment, where the average leaf area per plant for 5377 was approximately three times that for 5260.

Average individual leaf area was approximately the same for 5260 and 5339 in both the 13- and 14-hour photoperiods (45.8 and 63.7 cm^2, respectively), with 5377 showing an increase in the 14-hour treatment (55.7 cm^2 in 13-hour, 79.3 cm^2 in 14-hour). All values increased in the 15-hour treatment, with 5377 showing the largest value (151.4 cm^2), followed by 5339 (130.9 cm^2) and lastly 5260 (67.1 cm^2). Mean square values for growth chamber harvest data are shown in Table 18.

Summary of clonal performance in controlled environment

To compare clonal performance, clones were ranked first, second or third for each variable at the end of the growing period; the order in which they are presented in the following discussion indicates their ranks. The one six-week growth period was combined with the three growing periods of seven and one-half weeks and the pooled means were used as a basis of comparison. Thus each mean value represented 12 trees (3 trees per clone x 4 replications).

In the 13-hour photoperiod, the ranking was 5377, 5339 and 5260 for the variables stem height, stem diameter, leaf weight, leaf number and

Table 18. Mean square values for photoperiod by variable for growth chamber harvest date

Source	DF	Dependent variables						
		SH (cm)	SD (in)	LN	SW (gm)	TIW (gm)	LA_2 (cm^2)	LN
		<.01	.06	<.01	<.01	.01	.02	.03
Photoperiod	2	24222.70	0.93	707.77	368.25	2033.41	61619276.80	1137.22
Error	6	11529.36	0.20	49.63	18.50	192.25	7461711.80	175.77

total top dry weight, whereas the leaf area ranking was 5339, 5377 and 5260; stem weight ranking was 5377, 5260 and 5339.

In the 14-hour treatment, the ranking was again 5377, 5339 and 5260 for the variables leaf number, leaf weight, leaf area, stem weight and total top dry weight but the stem diameter ranking was 5377, 5260 and 5339. Stem height exhibited a third order: 5339, 5377 and 5260.

In the 15-hour photoperiod, the ranking was 5377, 5339 and 5260 for leaf weight, leaf area and total top dry weight; it was 5377, 5260 and 5339 for stem height, stem diameter, stem weight and leaf number.

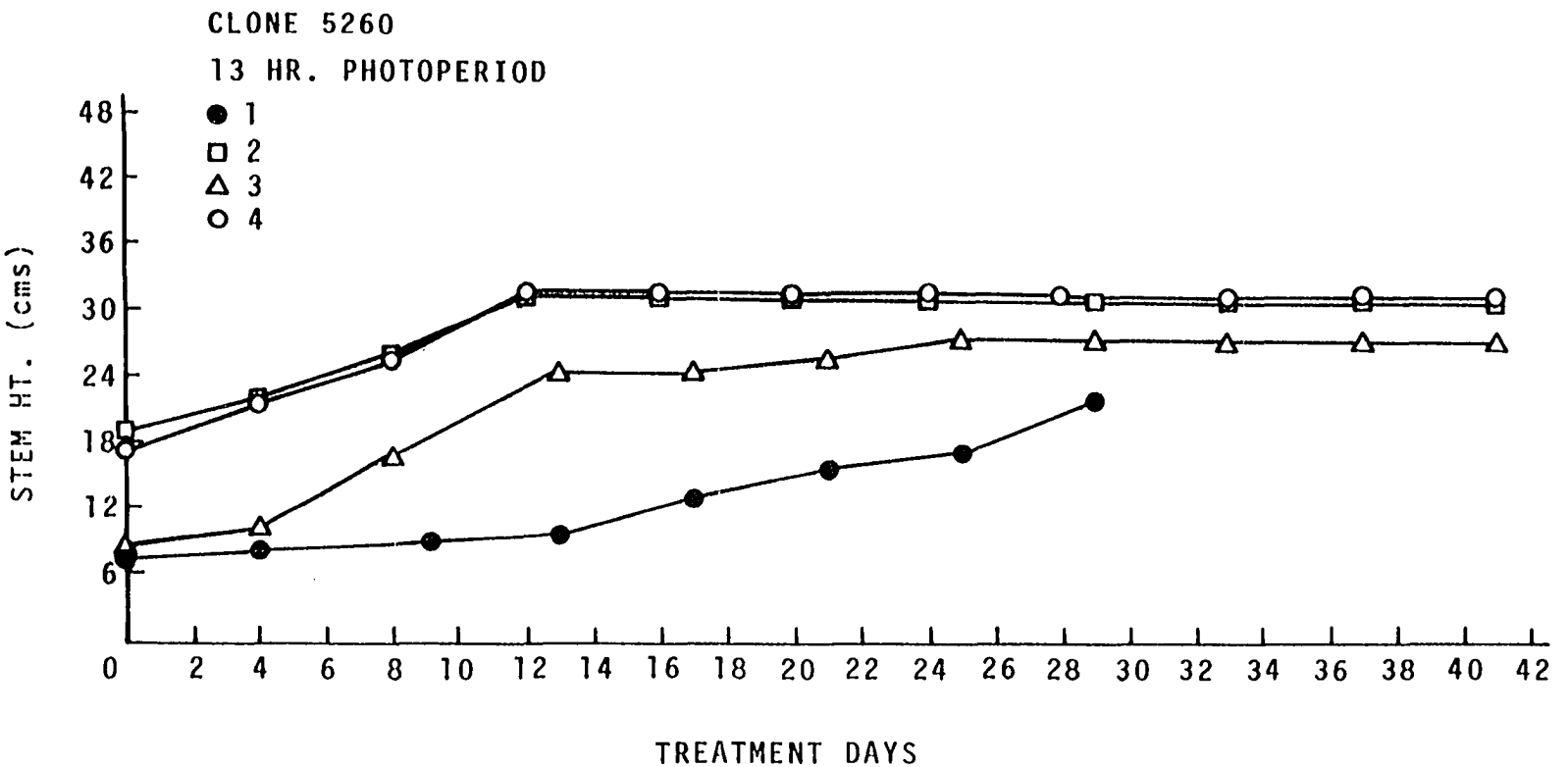
Thus 5377 ranked first in all variables except 13-hour leaf area and 14-hour stem height. 5260 ranked last in 15 of the 21 measurements. Differences among clones were smallest in the 13-hour photoperiod, greater in the 14-hour treatment and usually greatest in the 15-hour photoperiod.

Growth Chamber Growth: Periodic Measurement of Height and Leaf Number

Measurements of stem height and leaf number were taken at approximately four-day intervals on all material grown in the controlled environments for each replication. The mean value of three trees per clone was used as a basis of comparison. The first replication was shorter than the others, so trees there were measured only eight times compared with 11 times for the other three runs.

Height growth of 5260 showed approximately the same trends in both the 13-hour and 14-hour photoperiods (Figures 25 and 28). Clone 5260 generally grew approximately three weeks and then set bud, resulting in cessation of further height or leaf number increases. Final height values were

Figure 25. Mean stem height (cms) for clone 5260, in 13-hour photoperiod, by replication. Each measurement time for Figures 25 to 33 equals approximately four days on this and subsequent tables. N = 3


CLONE 5260
13 HR. PHOTOPERIOD
1
2
3
4
STEM HT. (cms)
48
42
36
30
24
18
12
6
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
TREATMENT DAYS

similar in both photoperiods, although there were differences among replications. For example, 14-hour trees in the third replication were only about one-third as tall as those grown in the 13-hour treatment for the same replication (Figure 28).

In the 15-hour photoperiod, the rate of height growth was approximately the same through the first three weeks, as in the other photoperiods, but after this time 5260 increased further in height and leaf number and continued to grow approximately twice as long as in the two shorter photoperiods (Figure 31). There was less variation among replications in the 15-hour treatment compared to the 13- and 14-hour photoperiods.

Height growth of 5377 in the 13-hour treatment was similar to that of 5260; all plants generally grew approximately three weeks and then set bud (Figure 26). Unlike clone 5260, however, 5377 grew for a longer period of time in the 14-hour photoperiod than in the 13-hour photoperiod (generally through the sixth week) (Figure 29). Under the 15-hour photoperiod, growth of 5377 was rapid and all trees grew throughout the growing period (Figure 32). Final stem height values for 15-hour 5377 were significantly higher than that for either 15-hour 5260 or 5339 trees (Figures 31, 32 and 33).

In summary then, the growth for 5377 trees improved with increasing photoperiod. Relatively little variability existed among replication in both the 14-hour and 15-hour environments.

Clone 5339 grew longer in the 13-hour photoperiod than did 5260 or 5377; growth continued for approximately five weeks when all trees set bud (Figure 27). However, final height values for this photoperiod were approximately the same for all three clones.

Figure 26. Mean stem height (cms) for clone 5377 in 13-hour photoperiod

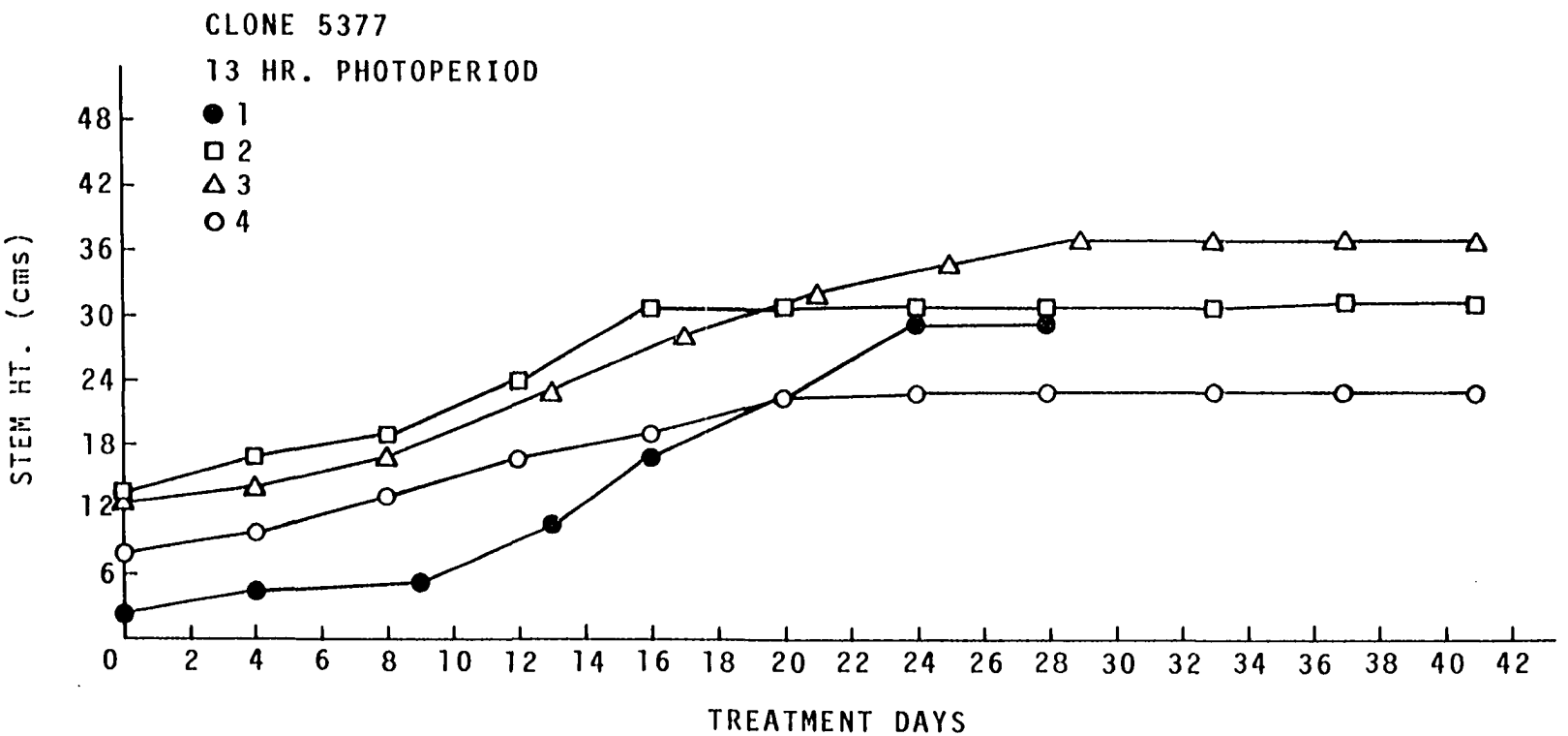

CLONE 5377
13 HR. PHOTOPERIOD
1
2
3
4
STEM HT. (cms)
48
42
36
30
24
18
12
6
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
TREATMENT DAYS

Figure 27. Mean stem height (cms) for clone 5339 in 13-hour photoperiod

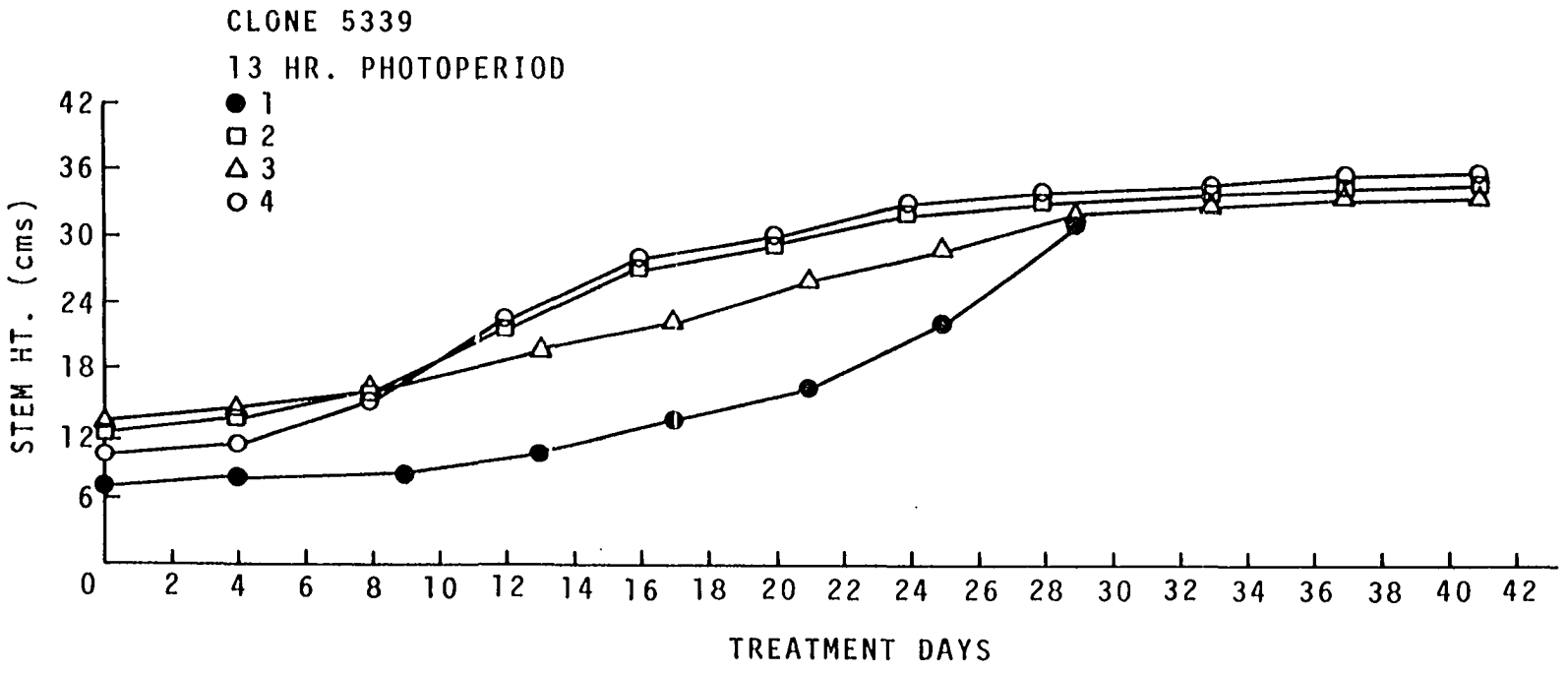

CLONE 5339
13 HR. PHOTOPERIOD
1
2
3
4
STEM HT. (cms)
42
36
30
24
18
12
6
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
TREATMENT DAYS

Figure 28. Mean stem height (cms) for clone 5260 in 14-hour photoperiod

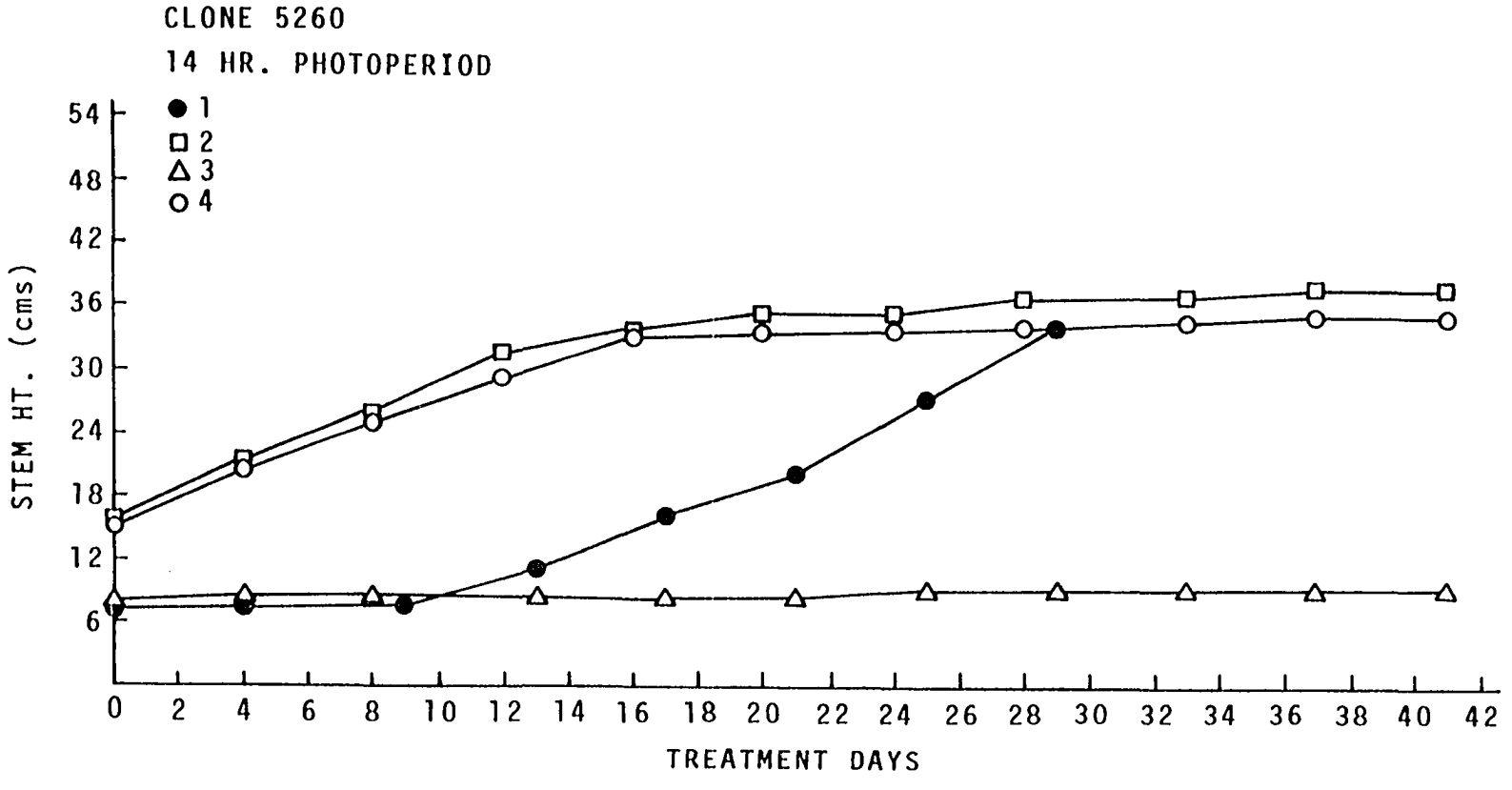
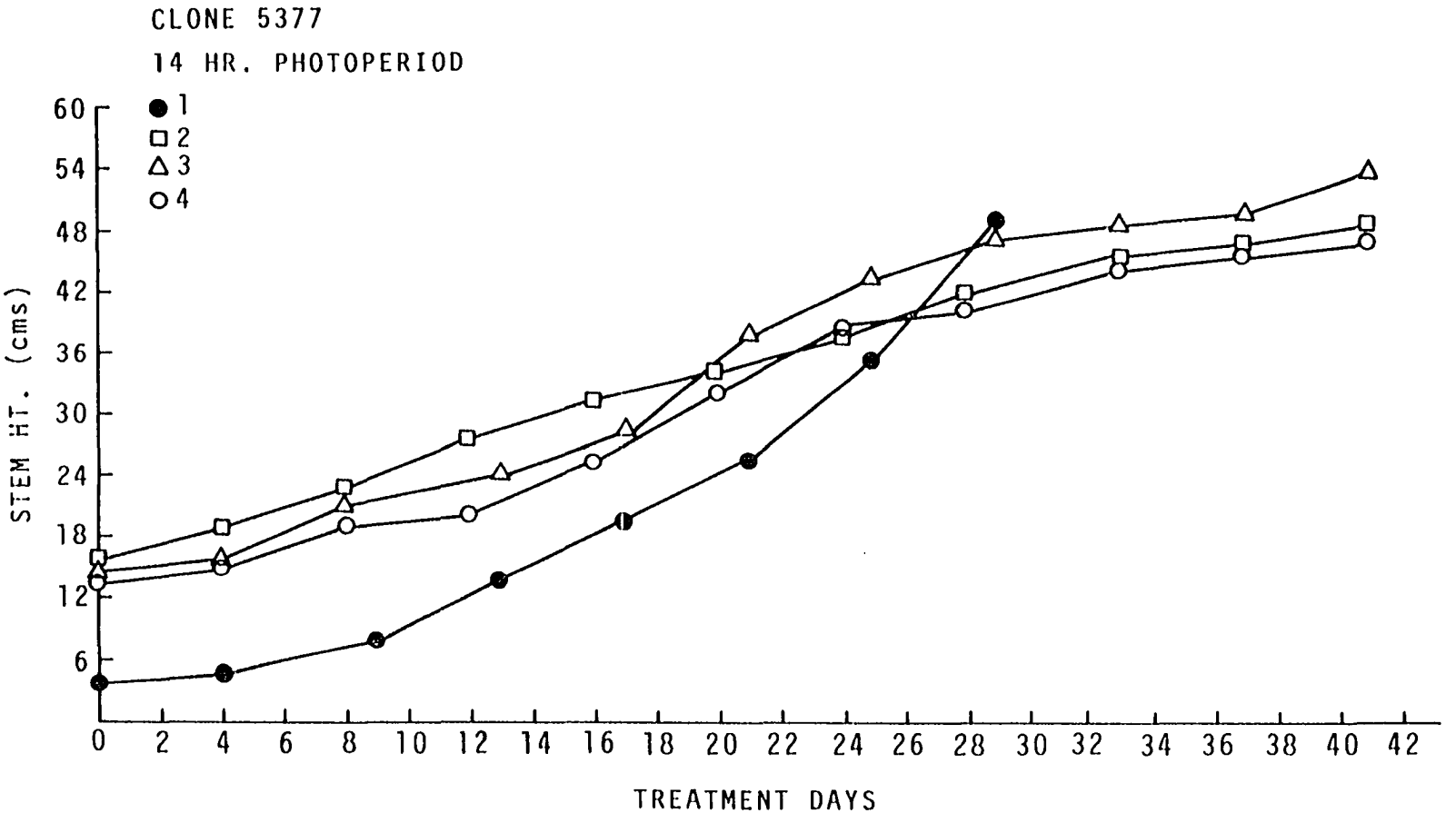

CLONE 5260
14 HR. PHOTOPERIOD
● 1
□ 2
△ 3
○ 4
STEM HT. (cms)
54
48
42
36
30
24
18
12
6
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
TREATMENT DAYS

Figure 29. Mean stem height (cms) for clone 5377 in 14-hour photoperiod


CLONE 5377
14 HR. PHOTOPERIOD
1
2
3
4
STEM HT. (cms)
60
54
48
42
36
30
24
18
12
6
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
TREATMENT DAYS

Rate and duration of height and leaf number growth were similar for 5339 in both the 14- and 15-hour photoperiods but final heights were larger under the longer day-length (Figures 30 and 33). Little variation occurred among replications for all three photoperiods.

Growth Chamber Growth: Summary of Periodic Measurement Results

There was little overall variation among replications in all photoperiods for all three clones. Trends generally were consistent and repeatable. In the 13-hour photoperiod, all three clones performed somewhat similarly; growth occurred through only part of the growing period followed by bud set. Height and leaf number final values were similar for all clones, although length of growing time varied from approximately three weeks for 5260 and 5377 to approximately five weeks for 5339 (Figures 25, 26 and 27).

In the 14-hour treatment, 5260 responded only slightly better than in the 13-hour treatment, whereas 5377 did somewhat better and growth of 5399 improved markedly. Final height ranking in the 14-hour photoperiod was 5339, 5377 and 5260 (Figures 28, 29 and 30).

In the 15-hour photoperiod, all three clones grew throughout the growth period (Figures 31, 32 and 33). In comparison with the 14-hour performance, 5260 made the greatest increase in growth percentage. However, final heights of 5377 trees were considerably greater in the 15-hour environment than those for 5260 or 5339.

Rankings based on the average final value from the periodic measurements generally agreed with those based on harvest data not only for the two common variables, stem height and leaf number, but also for all other variables measured at harvest time.

Figure 30. Mean stem height (cms) for clone 5339 in 14-hour photoperiod

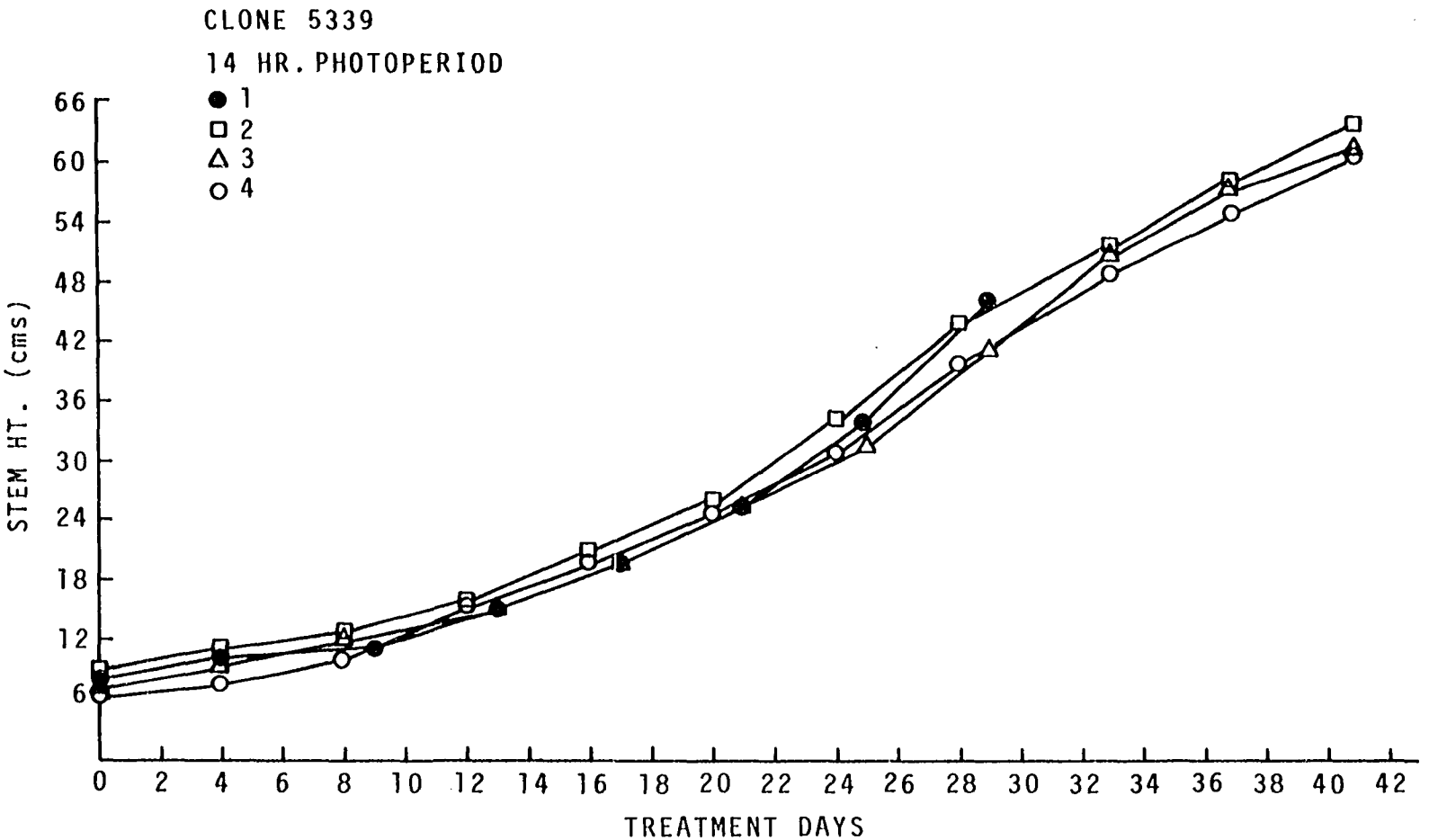

CLONE 5339
14 HR. PHOTOPERIOD
● 1
□ 2
△ 3
○ 4
STEM HT. (cms)
66
60
54
48
42
36
30
24
18
12
6
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
TREATMENT DAYS

Figure 31. Mean stem height (cms) for clone 5260 in 15-hour photoperiod

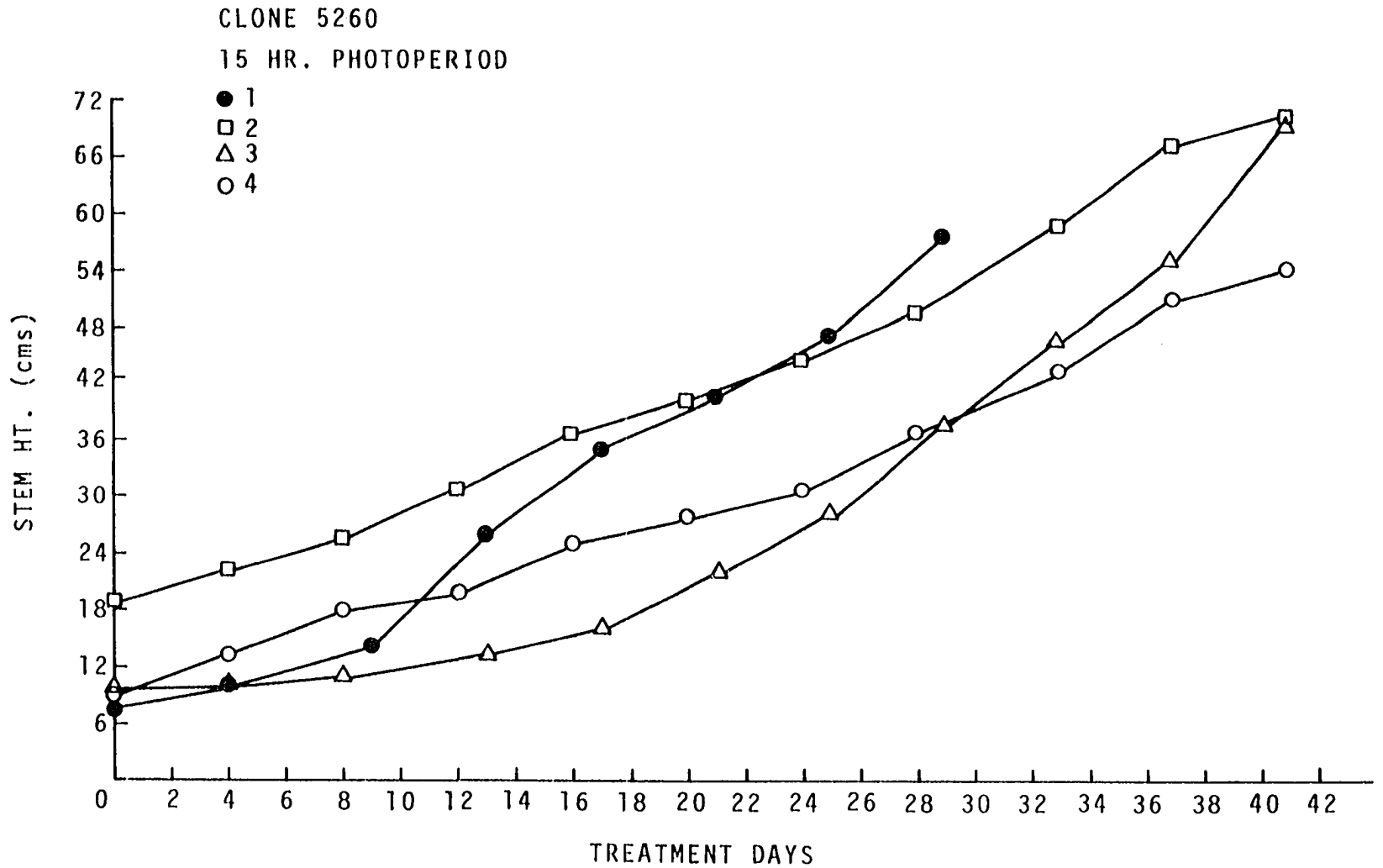

CLONE 5260
15 HR. PHOTOPERIOD
1
2
3
4
STEM HT. (cms)
72
66
60
54
48
42
36
30
24
18
12
6
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
TREATMENT DAYS

Figure 32. Mean stem height (cms) for clone 5377 in 15-hour photoperiod

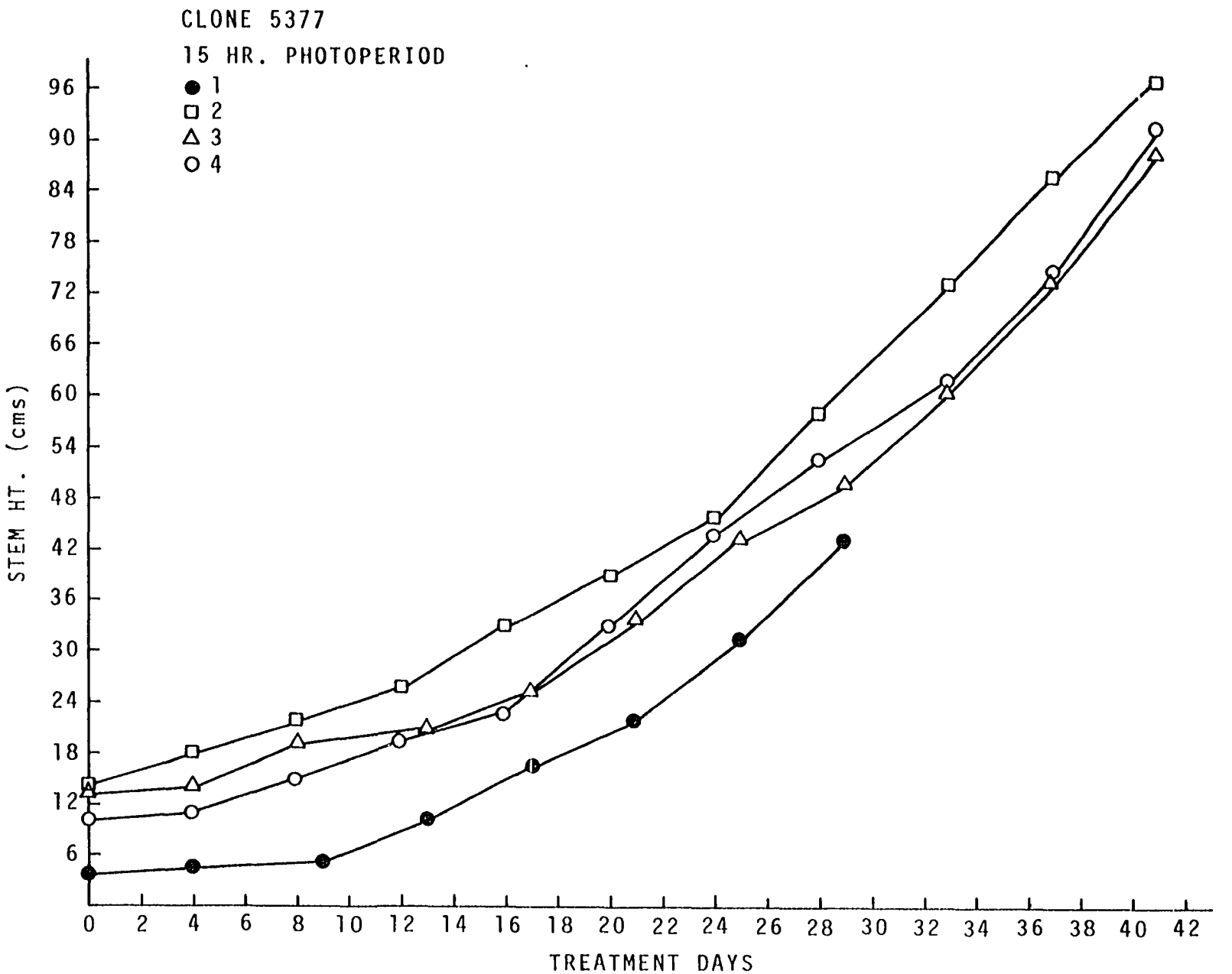
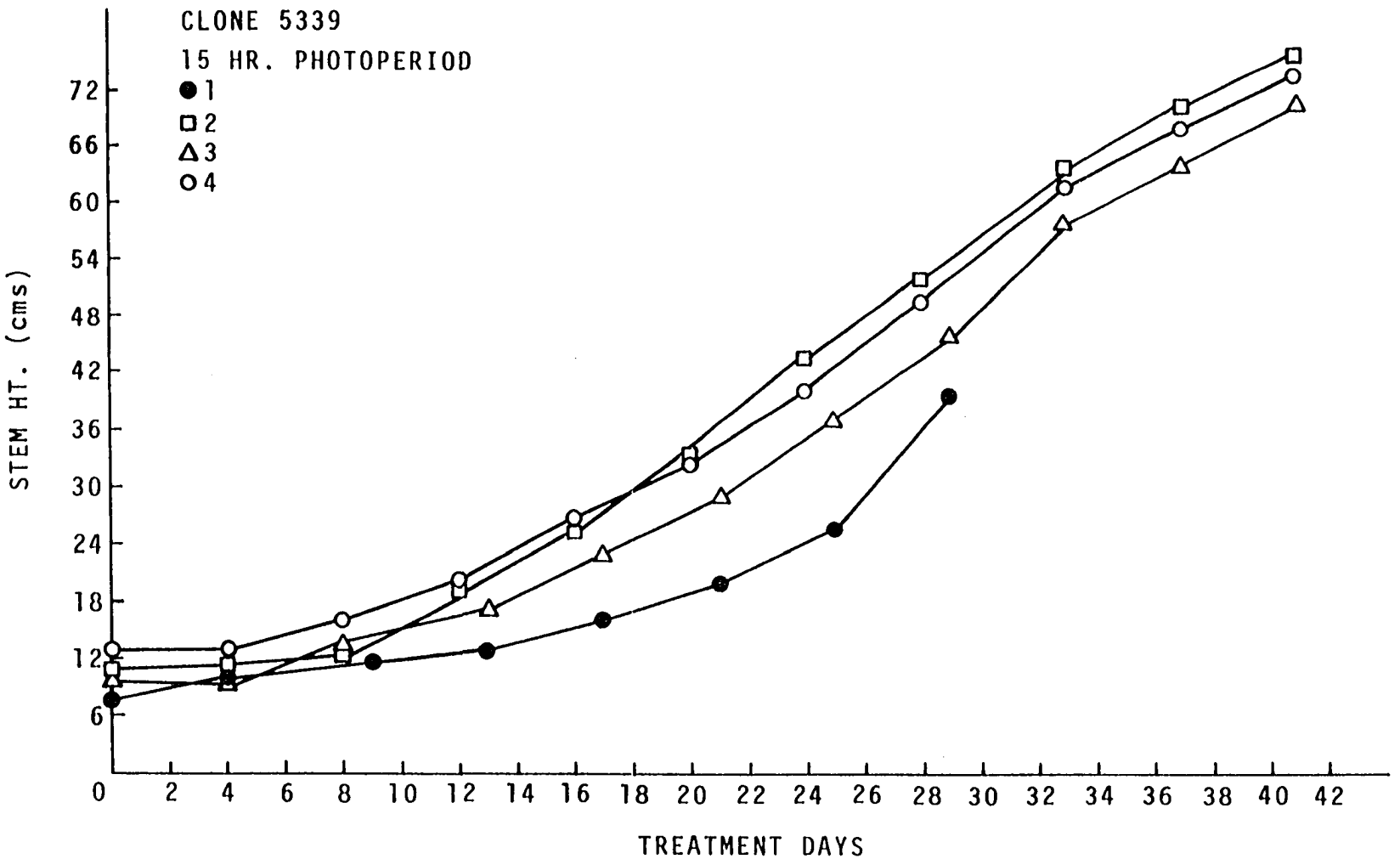

CLONE 5377
15 HR. PHOTOPERIOD
1
2
3
4
STEM HT. (cms)
96
90
84
78
72
66
60
54
48
42
36
30
24
18
12
6
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
TREATMENT DAYS

Figure 33. Mean stem height (cms) for clone 5339 in 15-hour photoperiod


CLONE 5339
15 HR. PHOTOPERIOD
1
2
3
4
STEM HT. (cms)
72
66
60
54
48
42
36
30
24
18
12
6
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
TREATMENT DAYS

Responses of the clones to the length of the photoperiod in the controlled environments were probably governed at least partially by the length of the photoperiod to which each was adapted in its native habitat. This will be discussed further in subsequent sections.

Correlations between Growth Room and Field Growth

To quantify the relationships between the growth chamber and the field for the measured variables, correlation matrices were calculated for three combinations of variables: (1) all variables within each field location, (2) all variables within each growth room photoperiod, (3) each variable in each field location with each variable in the different photoperiods. Thus it was possible to establish correlation coefficients, for example, between the average third harvest stem height over three years in Ames with the average stem height over four replications in a given photoperiodic treatment. Values are shown for both methods of calculation of the "r" values, as outlined in the methods section. These values appear in Table 19.

The 13-hour photoperiod yielded the poorest growth chamber-field correlations. Higher values of "r" were obtained between field growth and growth in the longer photoperiods. An average correlation value was also calculated ($\overline{XR}$) for each location and photoperiod; this value increased progressively with photoperiod for both locations. Values for the correlations between Ames field measurements and those of the three photoperiods were larger than those between Rhinelander field measurements and the same photoperiods.

Table 19. Correlation coefficients between growth chamber and field growth for first year (third harvest) growth measurements by growth chamber photoperiod and field location with clones and years pooled

	Growth chamber photoperiod (hrs)	Dependent variables							
		SH	SD	LW	SW	TTW	LA	LN	$\overline{XR}$[a]
Ames x	13	.82**	.44**	.44*	.90**	.57**	.31*	.60**	.58
	14	.33**	.91**	.79**	.82**	.83**	.79*	.81**	.75
	15	.80**	.85**	.86**	.90**	.88**	.78*	.89**	.85
Rhine x	13	.65	.34	.26*	.65	.34	.32*	.47	.43
	14	.30	.65	.70*	.53	.59	.69*	.66*	.59
	15	.61	.61	.56	.65	.59	.68*	.73*	.63
Locations combined	13	.74*	.39*	.35*	.78*	.46*	.32*	.54*	.51
	14	.32*	.78*	.75*	.68*	.71*	.74*	.74**	.67
	15	.71*	.73*	.71*	.78*	.74*	.73*	.81**	.74

[a] $\overline{XR}$ = mean correlation value.

* Significant at $P<.05$.

** Significant at $P<.01$.

calculated ($\overline{XR}$) for each location and photoperiod; this value increased progressively with photoperiod for both locations. Values for the correlations between Ames field measurements and those of the three photoperiods were larger than those between Rhinelander field measurements and the same photoperiods.

DISCUSSION

Field Productivity

The objective of this study was to develop a technique for rapid selection of those clones that might be expected to do best in given field locations by means of a preliminary analysis of selected variables under growth room conditions. This study attempted to define the relationship between growth room and field productivity for three hybrid poplars when only the photoperiodic conditions in the field were roughly approximated in the growth chamber. Clonal material was grown in the field at two separate locations for three different years, as well as in controlled environment chambers, in order to develop correlations between the field and growth chamber growth.

The growth of clone 5260 at the Ames location (near latitude 42° N) varied considerably among the three years the clones were in the field but the total top weight accumulated was similar for the years 1971 and 1972; values for 1973 were slightly lower. The most characteristic attribute of the growth of clone 5260 was that it consistently set bud shortly after the middle of the growing season (about August 1st); following this no further increases usually occurred in the magnitude of any of the seven measured variables, with the exception of a slight increase in average leaf area. The cambium may have been active following bud set, as reported for Pinus sylvestris by Wareing (1951), although significant increases in diameter were not detected between harvest intervals following the cessation of extension growth. Preceding bud set, 5260 usually grew faster than 5339 but was slower than 5377. Clones 5339 and 5377 continued to grow throughout the season for all three replications of first year growth trials; this

resulted in 5260 generally ranking in last place for all measured variables (1971 and 1973) or in second place (1972) at both locations.

The growth of clone 5260 might most easily be explained by assuming that the clone is photoperiodically and thermoperiodically adapted to southern Canada (latitude 51° N). When planted at Ames, 5260 was moved approximately 9° south of the native habitat of one of its parents. As Vaartaja (1960a) pointed out, at northern sites a long-day photoperiod still exists when the temperature is cold enough to require dormancy. When trees adapted to that site are transferred south into shorter days, the result is early dormancy although the temperature is still favorable for growth. When the photoperiod occurs in Canada that was found at Ames at approximately the first of August, clone 5260 would have already set bud. This clone is native to a region where climatic conditions are severe; because of its adaption to a stimulus occurring under long-day conditions as a cue for initiating dormancy processes, the clone does not make full use of the growing season. This is even more apparent when the clone is grown at a southerly site, as it was when planted at Ames. Thus, as Wareing (1956) pointed out, selection presumably has operated on the genotype to give the optimum duration of extension growth under the day-lengths prevailing at the native habitat. Transferring the species into shorter days alters the period of active growth.

The behavior of 5260 in Ames agrees with reports of other workers who have studied plants in relation to both photo- and thermoperiodic ecotypes. Vaartaja (1954, 1960b, 1962) found that northern species grew best in longer days and further that in northern ecotypes dormancy is induced by a longer day-length than in southern ecotypes. The farther north the origin

of the species, the more was the growth suppressed by a shorter (more southern) day-length. Other workers, Pauley (1952, 1957), Downs and Borthwick (1956), Downs and Piringer (1958), Pauley and Perry (1954), Kramer (1936), Vegis (1964), Sylven (1940), Wareing (1949a, 1969) and Wassink and Weirsma (1955), all reported that the time of height growth cessation was inversely correlated with the latitude of the native habitat; when northern strains were grown in the south, they showed reduced growth and stunting. Wareing (1956) pointed out that new forest types for any location must show the same delicate adjustment to day-length as is found in the native ecotype.

Other factors besides the photoperiod may have affected the growth of 5260 at the Ames location. Wareing (1969) reported that even in the case of Populus, where shoot growth (at the adapted site) may continue until the short days of autumn, it is possible that other seasonal factors besides the photoperiod may be involved in determining the duration of extension growth. Wareing (1949b, 1956, 1969) and Wareing and Saunders (1971) stated that water relations or soil fertility may impose limits on tree growth. However, at both sites, plants were irrigated and fertilized regularly, so this was probably not a primary cause of early bud set. Higher temperatures in the summer months at Ames, compared to the native site, may have also interacted with the photoperiod to produce an early cessation of height growth. Holst and Yeatman (1961), for example, presented evidence for the interaction of photo- and thermoperiods in regulating growth of jack pine.

At Rhinelander, 5260 had also been transferred south of its natural habitat but not as far south as when planted at Ames. Consequently, 5260

grew for a slightly longer time at the northern location. Following bud set, growth slowed for all measured variables. In the two years of "full season" growth periods at Rhinelander, 5260 grew in about the same fashion, although there were large differences in total photosynthate accumulated between the two years. Final harvest means measured on the seven variables for 5260 were comparable for trees planted at Ames all three years and those planted in Rhinelander in 1973; trees at Rhinelander in 1972 were significantly larger than those of the other years. Climatic variations may have influenced physiological processes that affected growth. For example, temperatures in 1972 for the months June through October were all below those for the same period in 1973 and below ten-year average temperatures for the same months. Perhaps lower temperatures resulted in reduced respiratory losses thus leading to greater net accumulation of photosynthate by 5260. Rates of photosynthesis and respiration were not measured in the field to substantiate this hypothesis, however. Other climatic data, such as the percent possible sunshine days and total radiation received, were not recorded for the years being compared. Cuttings planted in the years the study was replicated were similar in size and appearance and were all taken from stock plants at approximately the same time each year.

Root characteristics were not observed in the material that was harvested at monthly intervals. This data, coupled with measurements of rates of photosynthesis and respiration on field material, would have been valuable in examining the behavior of 5260 in relation to its early setting of buds. One untested hypothesis, for example, is that top growth of the trees of the 5260 was being inhibited more than photosynthetic rates,

resulting in a subsequent shunt of photosynthate to the root zone following the time of early bud set. One measured variable that did increase following bud set was leaf area; this was due to the expansion of leaves still not fully expanded at the time of bud set.

Clone 5377 is a hybrid from the central Wisconsin area. Consequently, when planted at the Ames and Rhinelander sites, it was not far removed from its adapted habitat, as contrasted with the movement of 5260. In Ames 5377 grew throughout the growing season all three years; rates of growth showed some variation between years, as seen from the bi-monthly measurement data. Largest differences occurred between years with respect to the variables stem and leaf dry weights and thus also total trop dry weight. That diameter growth was approximately the same for the years 1972 and 1973 at Ames, while large differences occurred in stem dry weights, might be explained by the fact that diameter measurements were made only at the base of the tree; differences in taper of the stem between trees would not have been detected by this one measurement.

In Ames 5377 ranked first for all variables measured for all harvest times for all three years. Thus, 5377 outgrew the more nearly native 5339 in all categories. These growth differences are less clearly explained in terms of a photoperiodic adaption to a native site. Although 5377 was moved south of its native habitat, it probably was still within reasonable limits of movement. Several workers have suggested that plants may be moved safely up to a few hundred miles from the native habitat (Gevorkiantz and Roe, 1935; Vaartaja, 1959; Holst and Yeatman, 1961). Perhaps 5377 is genetically a faster growing clone in the initial stages of growth. It is also possible that 5339 was preferentially investing photosynthate in roots

rather than in the other measured variables. Growth of 5377 in 1972 at Ames started slowly but by the time of the second harvest, dry weights had increased 12 times over the first harvest values; stem heights also showed an increase. Climatic variation may have caused this behavior. The average monthly temperature and the percent possible sunshine days were both below the ten-year average for 1972 at Ames.

Large differences occurred between the clones with respect to leaf area, number and dry weight at Ames. Clone 5377 was larger in these variables at all harvests, as compared to clones 5339 and 5260 at Ames. Again, these differences may have been related to clonal differences in rates of photosynthesis and respiration (light and dark).

At Rhinelander the growth of 5377 showed approximately the same trends for the two "full season" replications (1972 and 1973), although differences did occur with respect to all variables measured. Growth of clones 5260 and 5377 was approximately the same in Rhinelander until the second harvest in 1972, although there were differences in leaf characteristics. The fact that 5377 far surpassed 5260 by the final harvest was mostly because 5260 set bud early in the season and, therefore, did not fully utilize the growing time available. There also may have been clonal differences in genetic potential and rates of photosynthesis and respiration. In general 5377 showed large increases in growth of most measured variables in the second half of the growing season. This may have been related to the weight, area and distribution of leaves. In 1973, for example, large increases in leaf weight and area occurred between the second and third harvest times, while leaf number showed little increase. Perhaps by the time of the second harvest an optimum number and arrangement of leaves had

been formed for the most rapid photosynthesis with the least mutual shading, resulting in more rapid growth. It is equally possible that the trees were benefiting from an early investment of photosynthate into roots, resulting in an increased root surface area for water and nutrient uptake.

Rankings for 5377 at Rhinelander were similar to those at Ames; the clone ranked first for the majority of the variables measured for all harvests for all three years. However, growth patterns were dissimilar between the two sites. In 1972, 5377 generally grew better at Rhinelander, while in 1973 growth was better at Ames. For example in 1973 clone 5377 had approximately the same leaf area at both Ames and Rhinelander by the time of the third harvest, while stem weights at Ames were more than three times larger than those at Rhinelander and the leaf number and leaf weights were also significantly larger for the trees at Ames. Perhaps larger stem dry weights occurred because those trees in Ames formed more small leaves in an optically dense and optimally arranged pattern on branches for more efficient capture of solar energy.

Complete climatological comparisons between the locations were not possible due to the absence of published data; however, temperature data showed that although the temperatures for the months of June through September were higher at Ames, compared to Rhinelander, they were higher by about the same amount for those months in both 1972 and 1973 (mean of 8.2° F higher in Ames in 1972, mean of 7.2° F higher in Ames in 1973). Thus, growth differences between the two years were probably not due to differences in temperatures. Trees at both planting sites were irrigated as needed to keep soil moisture levels high. Further, plots at both locations were kept free of weed competition and were fertilized. Perhaps

inherent soil properties or differences in fertility levels led to some of the growth differences between the two locations. Although differences existed in cultural levels between Ames and Rhinelander, Rose and Promnitz (1975) showed that hybrid poplars grow well at Ames under conditions similar to ones used in this study.

Clone 5339 is a naturally occurring hybrid native to southern Iowa. Therefore, when planted at Ames, it was well within its adapted range, while at Rhinelander it had been moved north approximately three degrees latitude. Based on the theory of photoperiodic ecotypes, growth of 5339 at Rhinelander might have been expected to exceed that at the Ames location by virtue of the longer summer day-lengths at the more northern site. However, this was not the case for all variables measured. In examining the two "full season" growing periods at both locations (1972 and 1973), it was seen that 5339 grew differently in different years with respect to many of the variables measured and that no clear pattern of growth differences existed between years or locations.

Many workers have shown that when plants from more southern regions are moved northward, increased height growth results from delayed dormancy but plants are often injured by frost (Wareing, 1949a; Pauley, 1957). Equal day-lengths occur at Ames and Rhinelander on September 21 (12 hours, 15 minutes) and following this date the length of the day is longer at Ames until the next spring. The data of the third harvest at Rhinelander was very close to this date (September 21, 13 and 14 for the years 1971, 1972 and 1973, respectively). At the time of each of these harvests, 5339 had already set bud. Thus, clone 5339, even when moved northward approximately three degrees latitude, still perceived the

slightly longer autumn photoperiod as a cue to set bud; therefore, growth differences between the two locations were not due to buds being set at a significantly later date than at Ames. Frost damage was not noticed on any of the trees of 5339 at Rhinelander.

Growth of 5339 was generally slow initially, as shown by the first harvest data from all replications. Perhaps this was due to a difference between the clones with respect to the photosynthetic efficiency of the young leaves or perhaps 5339 was allocating greater amounts of photosynthate into roots, as compared to the other two clones. However, in 1971 trees at Rhinelander were planted a month later (July 1) than in the other two years and following this late planting date the growth of clone 5339 was rapid. No significant difference among the years was noticed in size or quality of the rooted cuttings planted; therefore, the cause of the slow initial growth of 5339 when planted as the normal time (early June) may have been due to some environmental restriction.

Clone 5339 did not grow well at either location in 1972. Again, no visible difference was noted between that year and the other two in relation to rooted cutting characteristics. The average monthly temperatures for the months June through September were all below the ten-year average for both Ames and Rhinelander. In addition the total monthly precipitation was also above normal for the months July through September at both locations in 1972 and the monthly percent possible sunshine days was below the ten-year average for the months June through September at Ames. Corresponding data were not available for the Rhinelander site. Radiation totals for 1972 were also less than 1971 for the months June through August. In short the climate in 1972 was colder, wetter and less sunny

than normal at both Ames and Rhinelander. However, this deviation in climatic conditions did not have the obvious effect on the growth of the clones 5260 and 5377 that it did on 5339. In fact final harvest data showed that these two clones grew as good or better in 1972, as compared to the 1973 season, when data were adjusted for differences in harvest times between the two years. Clone 5260, however, set bud early in the growing season as usual. Thus, 5339 appeared to be less tolerant of cold, wet and cloudy conditions.

In comparing the growth behavior of 5339 and 5377 at Rhinelander, it was noted that in 1973 final harvest values showed that there was approximately only a 10% difference in height, diameter and leaf number whereas the average stem dry weight of 5377 was 58% heavier than stems of 5339. Although wood properties were not examined on the harvested material, preliminary investigations by other workers have indicated that there appear to be differences between these clones with respect to quantities of vessels and fibers, leading in turn to differences in specific gravity (Cheng and Bensend, Department of Forestry, Iowa State University). Various researchers have reported conflicting results with respect to the relationship between rate of growth and specific gravity of wood (Farmer and Wilcox, 1966; Kennedy, 1968; Einspahr, Benson and Harder, 1972; Mitchell, 1972). This relationship is currently being investigated by other workers for clonal material similar to that used in this study.

Differences were noted between locations with respect to the proportion of photosynthate allocated to the stem and to the leaves by each clone. Clone 5260 showed the most variation between years at Ames but the three-year average of stem dry weight as a percentage of total top dry

weight was 46% in Ames and 44% in Rhinelander. Most difference was seen in the behavior of 5339, which showed a three-year average of 52% stem weight in Ames and 37% in Rhinelander. In other words, 5339 at Rhinelander allocated significantly more photosynthate to leaves (48% in Ames, 64% in Rhinelander). An average individual leaf area or weight (total leaf area or weight divided by total number of leaves) was calculated for 5339 for three years in Ames and two years in Rhinelander. The results showed that the average individual leaf weight, when pooled over three years in Ames, was 0.29 gm and in Rhinelander it was 0.39 gm. It is not known how the total leaf dry weight was distributed over the total leaf number. For example it is possible that 5339 in Rhinelander had a few heavier leaves with the majority being lighter in weight. Trees at Ames had an average individual leaf area of 30.8 cm^2 when pooled over three years, while those at Rhinelander averaged 45.7 cm^2. Thus 5339 responded to the Rhinelander environment by forming larger leaves than when grown at Ames. Whether this was an effect of the photoperiod is not known. It is possible that the differences between clones and locations in average leaf characteristics were related to differences in photosynthetic capacity or efficiency that resulted in growth differences.

Trees that were not harvested at the end of a particular year were left at the growing site to obtain information about second and third year growth. In Ames 5260 continued to set bud very early in the growing season (approximately June 25); this resulted in those trees generally being considerably smaller than 5339 or 5377 by the end of both two and three years, based on both harvest and nondestructive bi-monthly measurements. This behavior was again probably due to the fact that 5260, when planted in

Ames, was transplanted very far south of its natural range and thus into a region of shorter day-lengths and higher mean temperatures during the growing season. In Rhinelander 5260 grew for a longer time than at Ames but set bud by the first of August. Again 5260 was always smaller than 5377 and usually smaller than 5339, based on both harvest and nondestructive bi-monthly measurements. The only exception to this ranking occurred in 1972 and was due to the very poor growth of 5339 and not to enhanced growth of clone 5260. Again the delayed action by 5260 in setting bud at Rhinelander compared to Ames was probably due to the longer day-lengths at the northern site. As a result of the longer growth period, stem dry weights for 5260 at Rhinelander were six times heavier than those at Ames after two years.

Clone 5377 grew throughout the growing season at both locations with the exception of the three-year-old trees at Ames which set bud a month earlier than those at Rhinelander. After two years in the field, 5377 ranked in first place at both locations for all variables measured based on harvest data (planted in 1972, harvested in 1973). According to nondestructive bi-monthly measurements made on trees planted in 1971 and measured in 1972, height growth of 5377 was approximately equal to that of 5339 at Ames, whereas in Rhinelander 5377 was clearly in first place. However, there were considerable differences between locations for 5377 harvested in 1973. For example after two years (planted 1972, measured 1973) average stem heights at Ames and Rhinelander were similar but the stem plus branch dry weight at Rhinelander was almost twice as heavy as that at Ames. Again this may have been due to clonal differences in wood properties. The proportion of the total weight allocated to the stem and to the branches is not

known; perhaps those trees in Rhinelander had a greater amount of photosynthate allocated to branches, thus causing the large difference in total top wood dry weight.

Clone 5339 grew in approximately the same fashion at both locations but after two years the trees were larger in Rhinelander for all variables measured, based on harvest data (planted 1972, harvested 1973). This was probably because this clone, when planted at Rhinelander, was moved north of its natural range into longer summer day-lengths. However, by the end of three years, 5339 was much larger in Ames for all variables measured. This growth lag at Ames may have been because a disproportionate amount of photosynthate was being allocated to the roots for the first two years. The rapid growth of 5339 in the third year at Ames, resulting in its being ranked in first place, refutes the suggestion made by Mohn and Randall (1971) that culling of Poplar clones could be made after two growing seasons.

In general after three years in the field, 5339 was larger at Ames; the unusual weather conditions experienced in 1972, which affected the first year growth of 5339 so greatly, did not seem to markedly inhibit the growth of the two-year-old material (planted in 1971, measured in 1972). Apparently 5339 is less sensitive to unfavorable growing conditions after it is established at the site. After three years 5377 grew slightly better at Rhinelander, while 5260 grew approximately the same at both locations. However, because of a photoperiodic adaption to long days, 5260 ranked in last place at both locations at the end of the three-year growing period.

Growth Chamber Productivity

The fact that the three clones used in this study were adapted to different photoperiodic regimes was reflected by their growth performance under the controlled environment conditions. Little difference existed between the clones for any of the measured variables when grown under the 13-hour photoperiod; growth proceeded for a short period of time, followed by bud set after three to four weeks. These results agreed with the work of Nitsch (1957b, 1961) who stated that for Populus spp. short days cause the transformation of leaf primordia into scales. Following bud set it is probable that the trees were in a state of imposed, or quiescent, dormancy as defined by Wareing (1969). In one instance 5260 was transferred into longer (15 hour) days subsequent to bud set under the short photoperiod. This resulted in bud break and growth resumption for many of the trees so treated. However, if there was a delay in transferring the trees into the longer days, fewer trees resumed growth. This agrees with Van der Veen (1951) and Vegis (1964) who found that if trees were chilled at 5° C for between six to eight weeks while under the 13-hour photoperiod, many trees broke bud.

The 13-hour photoperiod was shorter than that exhibited during most of the growing season days at any of the native habitats of the three clones used in this study. Clone 5339, adapted to a more southerly latitude and thus to shorter days during the growing season, grew for a slightly longer time under the 13-hour photoperiod, as compared to the other two clones. However, due to rapid initial growth, 5377 ranked in first place at the end of all growing periods.

Under the 14-hour treatment, 5260, adapted to long summer day-lengths, grew approximately the same amount as in the 13-hour treatment; this illustrated that a 14-hour day-length was still limiting growth of the variables measured. Growth of 5377, adapted to a shorter summer day-length than 5260, grew somewhat better in the 14-hour photoperiod as compared to the 13-hour treatment. Clone 5339, adapted to the shortest summer day-lengths, grew markedly better in the 14-hour photoperiod. Under the 15-hour photoperiod, 5260 grew throughout the length of the measurement time. This clone showed the greatest percentage-wise increase in growth for all measured variables when grown under the 15-hour photoperiod, compared to the values found under the 14-hour photoperiod. Clones 5377 and 5339 also grew the largest in the 15-hour photoperiod, compared to the other two photoperiodic treatments. Thus, the growth of the clones generally improved with increasing photoperiod. This agreed with the work done by Larsen (1947) on grasses. Further the amount of improvement in growth of the clones with increasing photoperiod was related to the length of the photoperiod at the native habitat. Clone 5339, native to the most southern latitude and thus the shortest summer day-lengths, responded well when the photoperiod was increased from 13 to 14 hours, whereas 5260, native to the most northern latitude and thus the longest summer day-lengths, did not grow well until the photoperiod was increased to 15 hours. Clone 5377, native to a latitude approximately in the middle of these two clones, responded in a fashion intermediate to the other two clones with respect to stem height increase. The behavior of the clones in the different photoperiods illustrates McWilliam's (1966) point that controlled environments can be used to determine the adaptability of untested material to different

sites and that information gained from this type of study could be used to predict where a plant would not be likely to succeed. Further, results in this study agreed with Kramer's (1936) statement that knowledge of the optimum photoperiod for a given species should aid in predicting whether or not it was suitable for a given latitude. There was also agreement with Yeatman (1965, 1967, 1974), who found in studying the effects of the interaction of the genotype and the environment on material grown both in the growth chamber and the field that the patterns of response in the field paralleled those seen in controlled growth chambers and that the growth behavior within the growth chamber showed an overall clinal pattern of genetic variation due to environmental adaptation. While Wareing (1956) pointed out that the demonstration of a photoperiodic response in relation to experimentally controlled day-lengths and light conditions does not imply that such effects will occur in nature, in this study the data from the controlled environment chambers and the field were consistent.

There was consistency in ranking between the three clones and photoperiods tested. Clone 5377 ranked in first place for all variables measured in all three photoperiodic treatments except for two variables. Clone 5260 ranked in last place for 15 of the 21 measurements made. Trends appeared to be consistent and repeatable between replications of the controlled environment study. The time of year the cuttings were taken from the stock plants did not have a significant relationship to the growth performance in the growth chambers, even though it is probable that the hormonal and nutrient status of the stock plant did change seasonally. Nitsch (1957a) reported a relationship between the photoperiodic regime to which the stock plants were exposed and the ability of cuttings to root, whereas

Wareing (1950a) reported no differences in rooting of cuttings taken from plants of Pinus sylvestris exposed to various photoperiods. Most variation between replications within a photoperiod occurred within the 14-hour treatment for clone 5260. It is possible that this photoperiod was near the threshhold for permitting full expression of genetic growth potential.

According to Carpenter (1966), the ideal controlled environment chamber should have uniform and reproducible conditions. While attempts were made in this study to eliminate variation between chambers, some minor differences in light intensity occurred. It is not known what effect this variation had on the production and distribution of assimilate within the trees. Many researchers have reported that variations in light intensity can affect shoot to root ratios, rates of photosynthesis and respiration and chlorophyll and nitrogen content of leaves for several woody species (Bourdeau and Laverick, 1958; Gordon, 1969; Hellmers, 1963; Loach, 1967).

Only one combination of day/night temperature was used in this study. The temperature used was based on the results of a previous study with clone 5339 (Domingo and Gordon, 1974). Perhaps this temperature was not the physiological optimum for the other two clones used in this work as they were adapted to different areas with differing temperature regimes. Although Yeatman (1965, 1967, 1974) found that the effect of temperature contributed little to provenance differentiation in work with controlled environments, studies of the effects of temperature regime on controlled environment growth of these clones should be made.

Correlation of Field and Growth Chamber Productivity

By examining the values in Table 19, it can be seen that the 13-hour photoperiod yielded the poorest growth chamber and field correlations. This would indicate that there was not as much discrimination in ranking of clones in this photoperiodic treatment as compared to the longer photoperiods. The results, in fact, showed that the magnitude of the difference in performance between the three clones was least in the 13-hour treatment. Higher "r" values were obtained between field and the 14-hour growth chamber performance, with the highest values being obtained between field and 15-hour growth. Greatest differences in performance between the clones were obtained in the growth room at the longer photoperiods. Two values of "r" were particularly low with reference to the Ames and growth chamber correlations: the 13-hour leaf area and the 14-hour stem height. These correlation values were low because these two variables showed a disruption in the rankings of material grown in the growth chamber. The usual ranking for all variables in all three photoperiods had 5337 in first place; for these two variables 5339 ranked in first place.

The magnitude of the calculated correlation coefficients between Ames and the 15-hour photoperiod agreed with other reports. Yeatman and Holst (1967), correlating dry weight of four-month-old seedlings in controlled environments with heights of the same population of jack pine after three and four years, found highly significant values of "r" at 0.86. These authors used only one photoperiod (15 hours) in their work. Schmidt (1957, 1963) stated that to be of predictive value correlation coefficients should approach or exceed 0.80. In this study correlations between the Ames and growth chamber productivity in both the 14- and 15-hour photoperiods ful-

filled Schmidt's requirements. It is possible that higher correlation values might have resulted if the clonal material used would have all been from the same taxonomic grouping. Yeatman and Holst (1967) found that selection at an early age for high performance at a later age based on relative rankings was only moderately successful. In this study there was consistency in ranking of clones between the growth room and the field for nearly each variable measured and the variability in the field, when averaged over several trials, was apparently not large enough to disrupt this ranking. More controlled environment work is needed to confidently predict growth performance for clonal material after three years in the field, however.

An average correlation value was calculated for each location and photoperiod; this value increased progressively by photoperiod for both locations. Values for the correlations between Ames and the three photoperiods were larger than those between Rhinelander and the three photoperiods. This may be because there was less difference between the first and second ranked clones at the Rhinelander location for many variables.

SUMMARY AND CONCLUSIONS

Three hybrid Poplar clones, native to different latitudes, were grown at two field locations and in controlled environment chambers to define the relationship between growth chamber and field productivity when only the photoperiodic conditions in the field were roughly approximated in the growth chamber.

In the field study measurements of stem height and leaf number were made bi-monthly along with destructive harvests at monthly intervals; seven variables were measured on each tree harvested. Plants that were not harvested in a particular year were left at the site to obtain information on second and third year growth. For the controlled environment study, clones were placed in photoperiods of 13, 14 or 15 hours with a 25/15^{o} C day/night temperature combination for six or seven and one-half weeks. Measurements of stem height and leaf number were taken periodically until the end of the growing period when all trees were harvested and measured as in the field study. Correlation matrices were calculated between all variables measured within each field location and between the growth chamber and each field location. The ultimate objective of this study was to develop a technique of rapid selection of those clones that might be expected to do best in given field locations by means of a preliminary analysis of selected variables under growth chamber conditions.

Possible explanations for the results, the implications of the results, and the related literature were discussed. Major findings were:

1) Controlled environments can be used to simplify the complex relationship of genotype-environment interactions to growth when only one com-

ponent of the environment, the photoperiod, is varied. This information can be used to more effectively match individual clones with optimum field environments.

2) Greatest differences among the clones in performance in the growth chamber were obtained with the longest photoperiodic treatment (15 hours). The magnitude of the difference in performance between the three clones was least in the shortest photoperiod (13 hours).

3) There was consistency in ranking of clones between the growth room and the field for most variables measured and the variability in the field, when averaged over several years, was apparently not large enough to disrupt this ranking.

4) The magnitude of the calculated correlation coefficients between field and growth chamber growth varied with the length of the photoperiodic treatment in the growth chambers; the values, on the average, were largest between the two field locations and the longest photoperiod. Lower values in certain instances were due to disruptions in the rankings or to smaller differences between the first and second ranked clones in the field.

5) More controlled environment research is needed to be able to confidently predict growth performance after three years in the field.

6) Further research in this area should include, in addition to the variables examined in this study, measurements of root characteristics and rates of photosynthesis and light and dark respiration both on trees grown in the field and trees grown in the growth chamber. The wood properties of the three clones should also be examined in detail to help explain clonal differences in stem dry weight.

7) Use of controlled environments as a tool for the rapid selection of Poplar clones to be used in woody plant agrisystems appears to have considerable potential. These facilities will enable large numbers of clones to be screened for initial genetic potential and to determine the adaptability of untested material to different sites. However, results from controlled environment studies should be used in conjunction with other selection indices based on photosynthetic rates, enzyme expression and measures of insect and disease resistance. The data acquired from these various techniques should be fitted into models to enable predictions to be made over a wide range of conditions. Until such models are constructed and field tested, the full potential of controlled environment selection will not be realized.

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